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VOLUME 86

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SUID-AFRIKAANSE MUSEUM

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THE TRUSTEES OF THE
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CAPE TOWN

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LIST OF CONTENTS

	Page
CURRIE, P. J. The osteology and relationships of <i>Tangasaurus mennelli</i> Haughton (Reptilia, Eosuchia). (Published May 1982.)	247
GOSLINER, T. M. The South African Janolidae (Mollusca, Nudibranchia) with the description of a new genus and two new species. (Published September 1981.)	1
GRINE, F. E. Description of some juvenile hominid specimens from Swartkrans, Transvaal. (Published October 1981.)	43
GRINE, F. E. Occlusal morphology of the mandibular permanent molars of the South African Negro and the Kalahari San (Bushman). (Published October 1981.)	157
GRINE, F. E. Relative sizes of the maxillary deciduous canine and central incisor teeth in the Kalahari San (Bushman) and South African Negro. (Published December 1981.)	229
GRINE, F. E. <i>see</i> VAN DEN HEEVER, J. A.	
KENNEDY, W. J., KLINGER, H. C. & SUMMESBERGER, H. Cretaceous faunas from Zululand and Natal, South Africa. Additional observations on the ammonite subfamily Texanitinae Collignon, 1948. (Published October 1981.)	115
KLEIN, R. G. <i>see</i> SCOTT, L.	
KLINGER, H. C. <i>see</i> KENNEDY, W. J.	
SCOTT, L. & KLEIN, R. G. A hyena-accumulated bone assemblage from Late Holocene deposits at Deelpan, Orange Free State. (Published December 1981.)	217
SUMMESBERGER, H. <i>see</i> KENNEDY, W. J.	
VAN DEN HEEVER, J. A. & GRINE, F. E. Dinocephalia type material in the South African Museum (Reptilia, Therapsida). (Published October 1981.)	73

NEW GENERIC NAMES PROPOSED IN THIS VOLUME

	<i>Page</i>
<i>Bonisa</i> Gosliner, 1981	17

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- FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* 74: 627-634.
- KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309-320.
- KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* 17 (4): 1-51.
- THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

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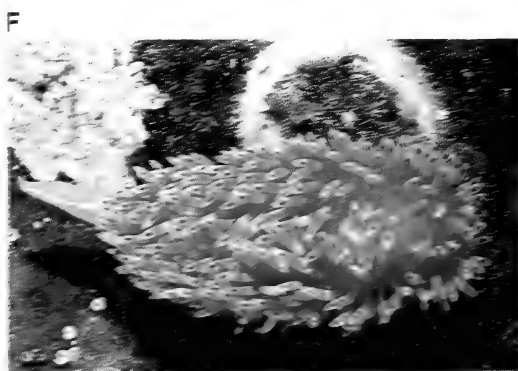
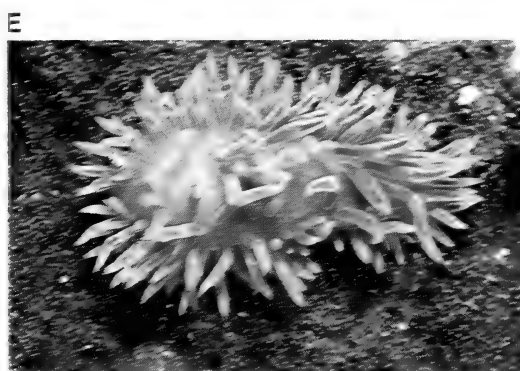
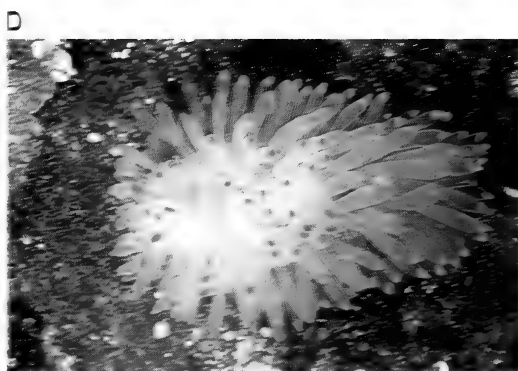
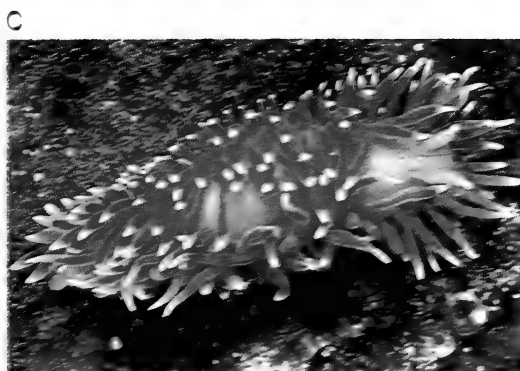
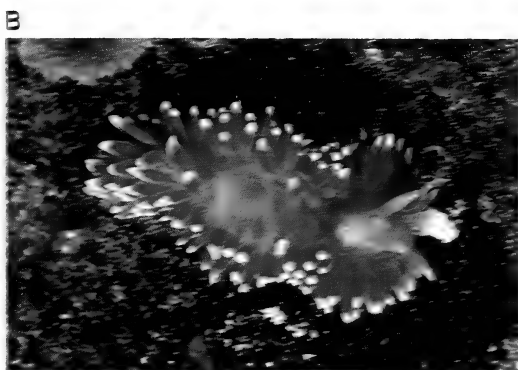
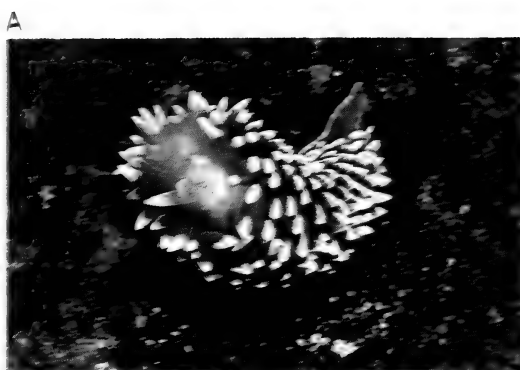


Fig. 1
A-B *Aeolidia cincta* Bergh 1907. C *Aeolidia cincta* sp. nov.
D-F *Aeolidia cincta* sp. nov.

ANNALS OF THE SOUTH AFRICAN MUSEUM
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THE SOUTH AFRICAN JANOLIDAE
(MOLLUSCA, NUDIBRANCHIA)
WITH THE DESCRIPTION OF A NEW GENUS
AND TWO NEW SPECIES

By

TERRENCE M. GOSLINER

Cape Town Kaapstad

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(MOLLUSCA, NUDIBRANCHIA)
WITH THE DESCRIPTION OF A NEW GENUS
AND TWO NEW SPECIES

By

TERRENCE M. GOSLINER

South African Museum, Cape Town

(With 28 figures and 3 tables)

[MS accepted 28 April 1981]

ABSTRACT

Examination of the shallow waters of the Cape Peninsula, South Africa, has revealed the presence of three sympatric species of Janolidae. The description of *Janolus capensis* Bergh, 1907 is expanded. *Janolus longidentatus* sp. nov. is described in detail and, despite its resemblance to *J. capensis*, possesses several consistently distinct morphological characteristics. The two species differ in body shape, position of the gonopore and nephroproct, dentition of the jaws and radula, arrangement of ganglia within the central nervous system, and in several aspects of reproductive morphology. The third species differs significantly from all other members of the Janolidae in that the digestive gland surrounds the stomach rather than entering the notum and cerata. *Bonisa nakaza* gen. et sp. nov. is described in detail. The presence of intermediate morphological characters in several species of janolids necessitates the synonymy of *Janolus* Bergh, 1884, and *Antiopella* Hoyle, 1902.

CONTENTS

	PAGE
Introduction.....	1
<i>Janolus capensis</i> Bergh, 1907	2
<i>Janolus longidentatus</i> sp. nov.	9
<i>Bonisa nakaza</i> gen. et sp. nov.	19
Discussion of the Janolidae	26
Acknowledgements	40
References	41

INTRODUCTION

The Janolidae are a family of arminacean nudibranchs consisting of 18 species in 5 genera. They are widely distributed in the temperate and tropical waters of the world. The genus *Caldukia* Burn & Miller, 1969, and the monotypic genus *Galeojanolus* Miller, 1971, are known only from Australia and New Zealand. *Proctonotus* Alder & Hancock, 1844, is also monotypic and has been reported only from Great Britain and the Brittany coast of France (Thompson & Brown 1976). *Antiopella* Hoyle, 1902, and *Janolus* Bergh, 1884, are much more widely distributed.

Bergh (1907) described *Janolus capensis* from three specimens dredged from False Bay, south-western Cape. Intertidal and subtidal collections by means of S.C.U.B.A. around the Cape Peninsula have yielded specimens of *Janolus capensis* as well as two previously unknown species, which are here described.

Antiopella and *Janolus* have been considered as distinct genera by most workers who have studied the Janolidae (Eliot 1906; Pruvot-Fol 1954; Marcus 1958; Burn & Miller 1969; Miller 1971). The South African species possess morphological features which are intermediate between those utilized to separate *Antiopella* from *Janolus*. For this reason, a review of the generic status of the Janolidae is provided. To supplement this review, specimens of *Janolus fuscus* from California, *J. cristatus* from England, and *J. toyamensis* from Hawaii were also examined.

Janolus capensis Bergh, 1907

Figs 1A–B, 2–9

Janolus capensis Bergh, 1907: 90, pl. 7 (figs 6–21). Barnard, 1927: 207, pl. 20 (figs 6–7).

Material examined

- 10 specimens, 20 m depth off Llandudno (34°01'S 18°20'E), 23 December 1979
- 6 specimens, intertidal, Clovelly, False Bay (34°05'S 18°26'E), 17–18 January 1980
- 3 specimens, 10 m depth, Rooi Els (34°18'S 18°49'E), 23 January 1980
- 1 specimen, 10 m depth, Castle Rocks, False Bay (34°18'S 18°29'E), 12 February 1980
- 5 specimens, 10 m depth, Windmill Beach, False Bay (34°12'S 18°27'E), 9 October 1980
- 2 specimens, 10 m depth, Rooi Els (34°18'S 18°49'E), 26 October 1980
- 2 specimens, 5 m depth, Miller's Point, False Bay (34°14'S 18°29'E), 28 October 1980

Distribution

Atlantic and Indian Ocean coasts of the Cape Peninsula, extending eastward to Rooi Els, Cape Hangklip.

External morphology

The living animals (Fig. 1A–B) attain a length of 30 mm. The stout body is broadest anteriorly, tapering to the acute posterior end of the foot. The rhinophores (Fig. 2A) are perfoliate with 11 to 16 complete or incomplete transverse lamellae. Between the rhinophores is the large, convoluted inter-rhinophoral crest (caruncle) (Fig. 2B). The anus in middorsal, near the posterior limit of the notum. The head (Fig. 2C) is rounded with the mouth situated

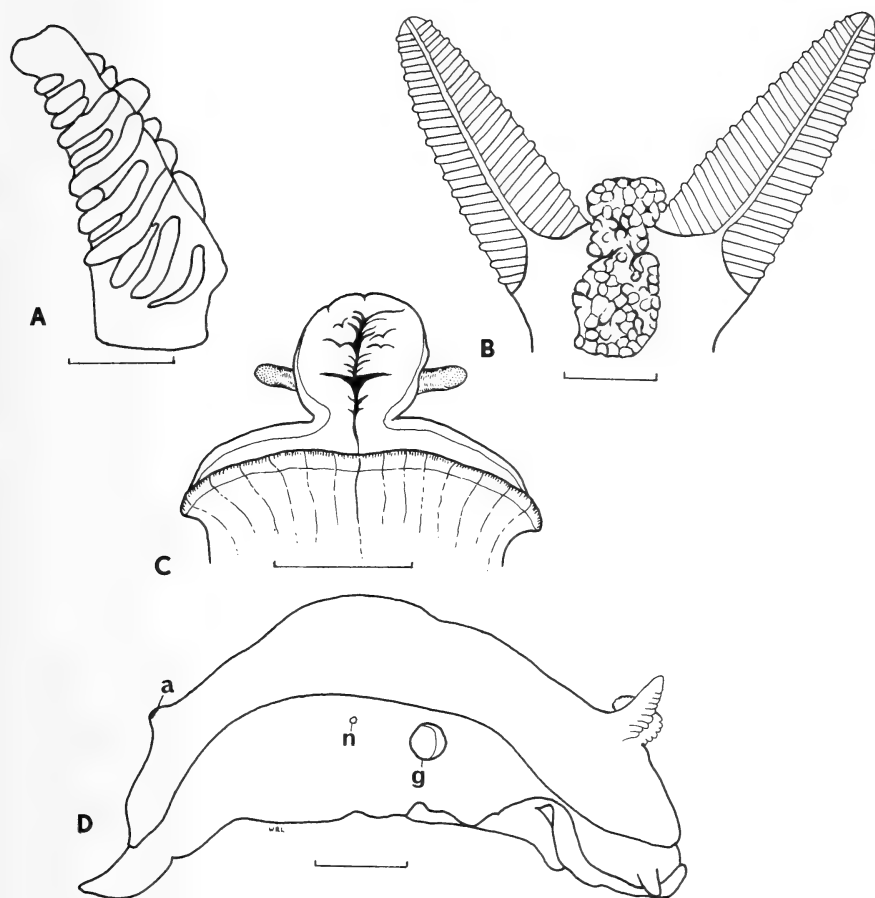


Fig. 2. *Janolus capensis* Bergh, 1907. A. Rhinophore, scale 1.0 mm. B. Inter-rhinophoral crest, scale 1.0 mm. C. Ventral view of head, scale 2.0 mm. D. Lateral view, scale 3.0 mm. Figs 2A-B, D are drawn from preserved material, Fig. 2C is from living material.

centrally. Short, blunt dorsoventrally flattened oral tentacles are present on either side of the head. The foot is rounded anteriorly with a deep transverse groove. The separate male and female gonopores are situated on the right side near the middle of the body, while the nephroproct is situated more posteriorly (Fig. 2D).

The cerata are entirely smooth, somewhat laterally compressed and are arranged in 5 to 6 closely packed longitudinal rows which are irregularly arranged. Within each ceras (Fig. 3A) are 2 to 4 irregular lobes of the digestive gland which branch near the middle of the ceras. The anteriormost cerata lack extensions of the digestive gland.

The ground colour is translucent white. Opaque white markings may be present or absent on the rhinophoral lamellae, inter-rhinophoral crest and

along the dorsolateral margin of the foot. The cerata are tipped with an apical band of opaque white guanine crystals which may have a bluish tinge. The digestive gland within the cerata varies from chocolate brown to brick red or red-orange.

Digestive system (Fig. 3B)

Near the opening of the mouth, numerous small, simple oral glands are present on the surface of the outer lips of the buccal mass. The buccal mass is large and muscular with an ovoid opening. A pair of large, highly dendritic

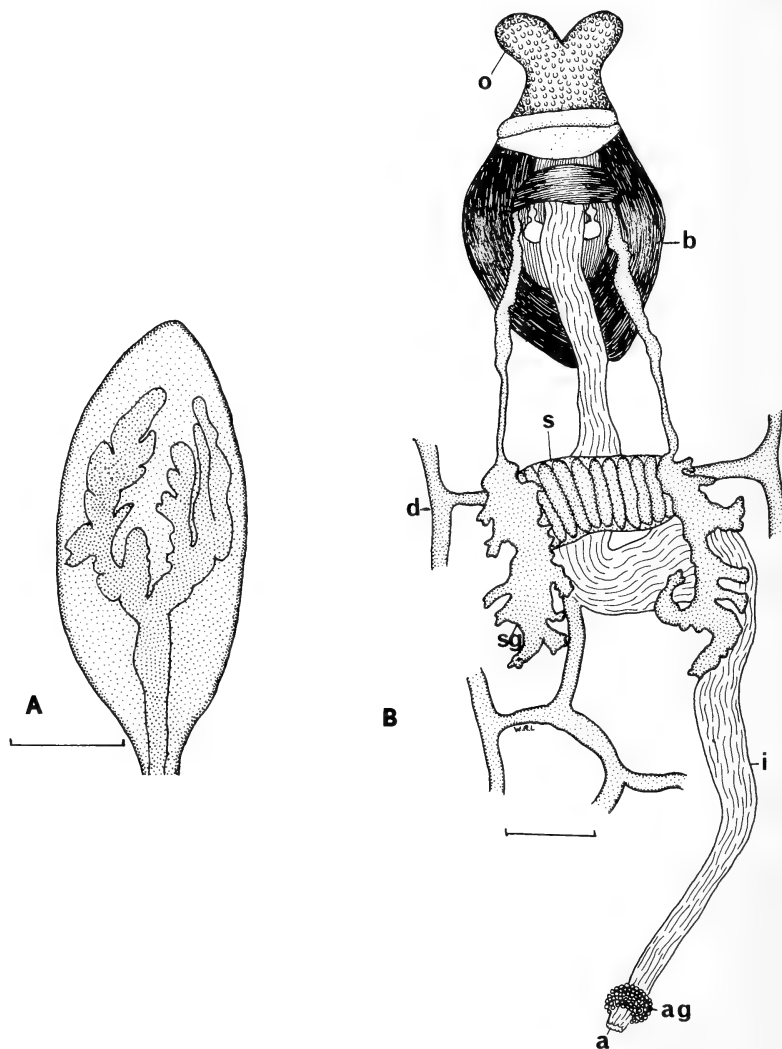


Fig. 3. *Janolus capensis* Bergh, 1907. A. Ceras dissected to show branching of digestive gland, scale 1,0 mm. B. Digestive system, scale 1,0 mm.

salivary glands extends anteriorly from the stomach and enters the buccal mass near its anterior limit via glandular ducts. The salivary glands are thick at their insertion, taper sharply and again expand into the dendritic portion. The oesophagus is wide throughout its length and enters the highly ridged stomach. Three major branches of the digestive gland emerge from the stomach. At the posterior limit of the stomach the intestine curves to the right and continues posteriorly, terminating at the medial anus. A well-developed anal gland surrounds the anus.

The buccal mass is large and muscular with an oblong opening (Fig. 4A). The paired jaws (Fig 4B) are large and strong. The inner masticatory border (Fig. 5A) is thickened and entirely smooth. There is a raised, arched portion which strengthens the masticatory edge.

The radula (Figs. 5B, 6) is broad and well developed. There may be from 17 to 21 rows of teeth with 26 to 42 lateral teeth on each side of the narrow, linear rachidian tooth. The hook-shaped lateral teeth (Fig. 6B) are smooth and sharply arched. Laterally from the centre of the radula, the lateral teeth increase in size until about one-third of the breadth of that half of the radula, at which point they again begin to diminish in size for the remaining outer two-thirds.

Central nervous system

All the major ganglia of the central nervous system (Fig. 7) are situated anteriorly in the circumoesophageal nerve ring. The cerebral and pleural ganglia are almost entirely fused, forming a pair of ganglionic masses separated by a short commissure. The anteriormost nerves on the dorsal surface of the

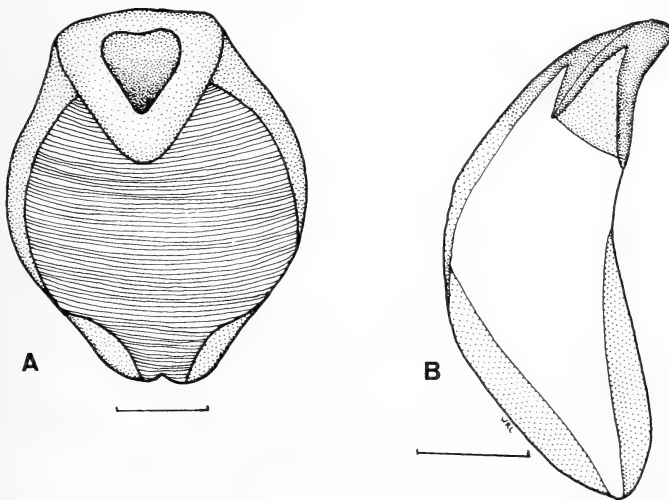


Fig. 4. *Janolus capensis* Bergh, 1907.

A. Buccal mass, scale 1,0 mm.

B. Jaw, scale 1,0 mm.



Fig. 5. *Janolus capensis* Bergh, 1907. A. Scanning electron micrograph of masticatory border of jaw, scale $300\ \mu\text{m}$ between squares. B. Scanning electron micrograph of radula, scale $10\ \mu\text{m}$ between squares.

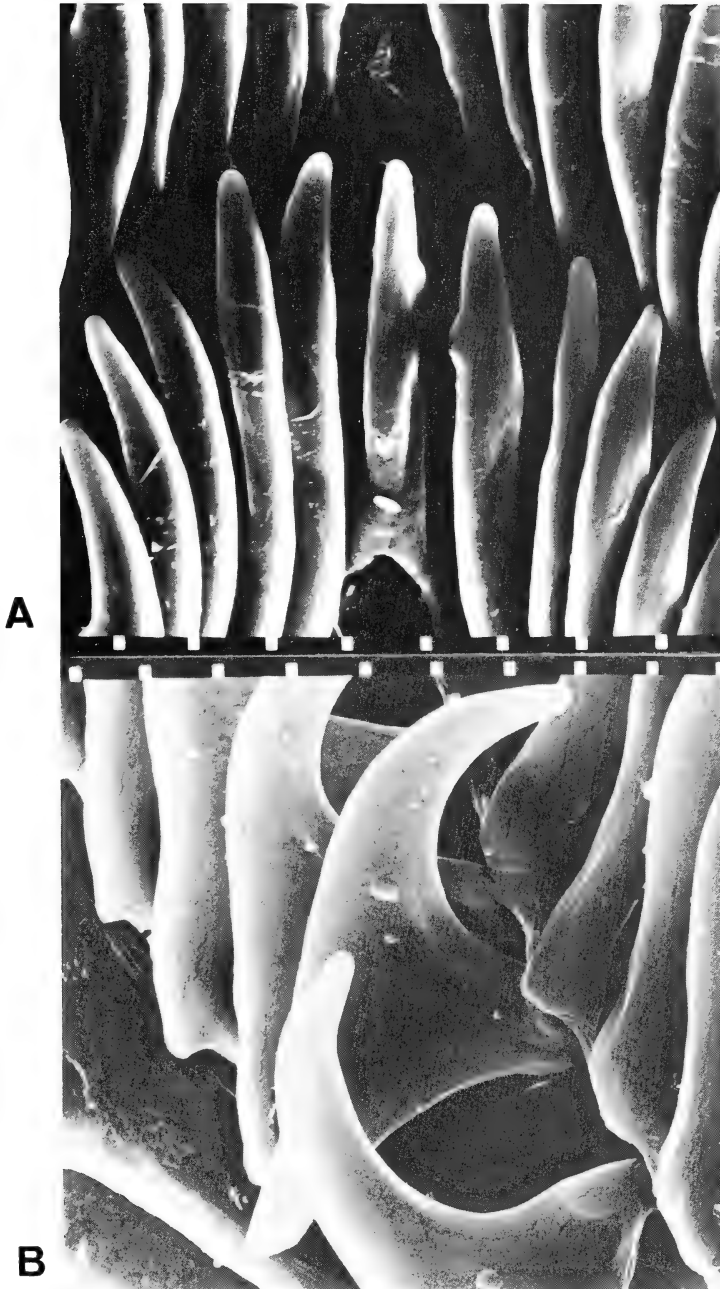


Fig. 6. *Janolus capensis* Bergh, 1907. A. Scanning electron micrograph of central portion of radula. B. Scanning electron micrograph of lateral tooth from outer portion of radula. Scales 10 μm between squares.

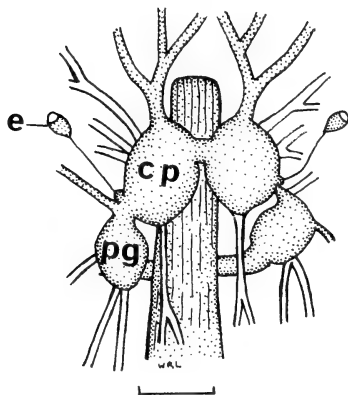


Fig. 7. *Janolus capensis* Bergh, 1907.
Central nervous system.
Scale 0,5 mm

cerebropleural ganglia bifurcate near the base. The outer branch innervates the rhinophore and a small rhinophoral ganglion is present near the apex of the nerve at the base of each rhinophore. The inner branch divides again with both branches innervating the inter-rhinophoral crest. The eyes are situated on short nerves which join the cerebropleural ganglia near their juncture with the somewhat smaller pedal ganglia. At the junction of each eye to the cerebropleural ganglia is a minute optic ganglion. Anterior to each buccal ganglion (Fig. 3B) is a minute gastro-oesophageal ganglion. The pedal ganglia are separated by a short commissure.

Reproductive system (Fig. 8)

The ovotestis consists of numerous lobes and gives rise to a slightly convoluted ampulla which subsequently narrows and bifurcates into the male

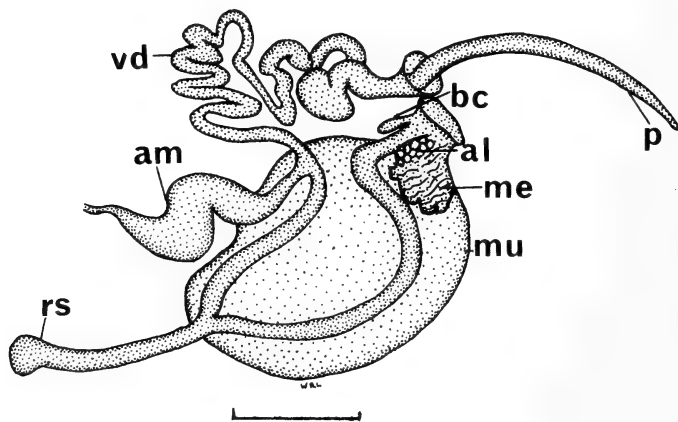


Fig. 8. *Janolus capensis* Bergh, 1907.
Reproductive system. Scale 4,0 mm.

and female ducts. The vas deferens is highly convoluted and prostatic throughout its length. It terminates at an elongate, acutely pointed penis. The extremely elongate oviduct is muscular and gives rise to a very long receptaculum seminis and continues until it joins the albumen gland of the female gland mass at the female atrium. *In situ*, the oviduct and receptaculum seminis are surrounded by the two lobes of the voluminous mucous gland. The membrane and albumen glands are significantly smaller than the mucous gland. Adjoining the oviduct and female gland mass, at the female atrium, is a small pyriform bursa copulatrix.

Egg mass

The egg mass (Fig. 9) is highly convoluted and corresponds to type B (Hurst 1967). There are 38 to 45 eggs per capsule.

Natural history

Janolus capensis is associated with, and feeds upon, several species of arborescent cheilostomatous ectoprocts, most commonly *Menipea triseriata* Busk, 1852, and *Onchoporella buskii* (Harmer, 1923). Mating individuals and egg masses are often found on ectoproct colonies as well. *Janolus capensis* is found commonly throughout the year along the Atlantic and Indian Ocean coasts of the Cape Peninsula from the intertidal to at least 40 m in depth.

Janolus longidentatus sp. nov.

Figs 1C, 10–17

Type material

Holotype—SAM-A34883, 1 specimen, 3 m depth, Miller's Point (34°14'S 18°29'E), 10 December 1980

Paratypes—SAM-A34884, 2 specimens, 10 m depth, Castle Rocks, False Bay (34°18'S 18°29'E), 1 October, 1980

SAM-A34885, 1 specimen, 5 m depth, Miller's Point, False Bay (34°14'S 18°29'E), 28 October 1980

Other material

3 specimens, intertidal, Clovelly, False Bay (34°05'S 18°26'E), 17 December 1979

2 specimens, 10 m depth, Windmill Beach, False Bay (34°12'S 18°29'E), 11 July 1980

Etymology

The epithet *longidentatus* refers to the elongate cusp of the lateral radular teeth which characterizes this species.

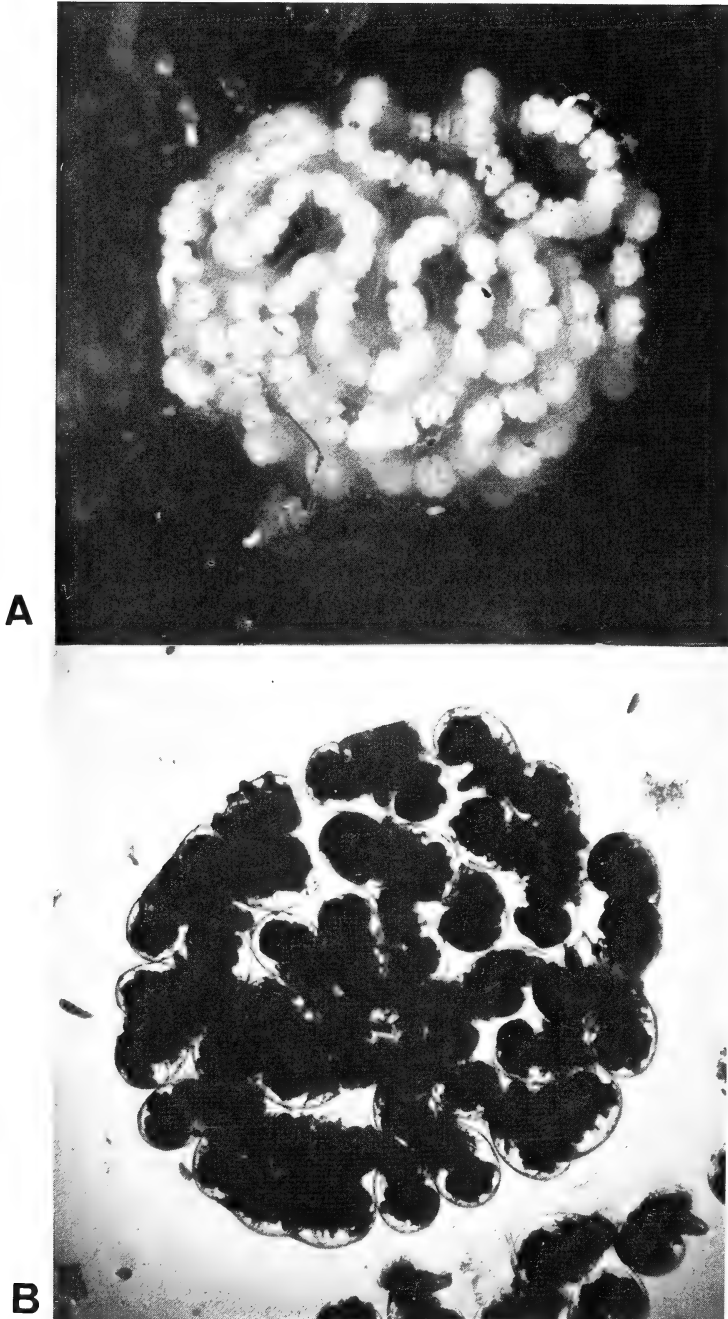


Fig. 9. *Janolus capensis* Bergh, 1907.

A. Egg mass $\times 6$.

B. Single egg capsule $\times 50$.

External morphology

Fully mature specimens (Fig. 1C) attain a maximum length of 20 mm. The slender body is widest anteriorly, tapering to an acute posterior margin of the foot. The rhinophores (Fig. 10A) are perfoliate with 9 to 12 complete or incomplete, transverse lamellae. The inter-rhinophoral crest (Fig. 10B) is highly convoluted, narrowest in the middle. The anus is situated mid-dorsally near the posterior end of the notum. The mouth is located centrally on the ventral side of the rounded head (Fig. 10C). A pair of short, blunt oral tentacles extend from either side of the head. The anteriorly rounded foot possesses a deep transverse groove at its anterior limit. The separate male and female gonopores are situated laterally in the anterior third of the right side of the body, while the nephroproct is located more posteriorly, but within the anterior half of the body (Fig. 10D).

The entirely smooth cerata are long and slender, arranged in 4 or 5 irregular, longitudinal rows. Within each ceras there are 2 main branches of the digestive gland which usually branch again above the base of the ceras (Fig. 11). The anteriormost cerata lack extensions of the digestive gland within them.

The general body colour of living animals is translucent white, with a pink or blue cast. Varying amounts of opaque white pigment are present on the rhinophores and at the apices of the cerata. The digestive gland within the cerata is chocolate brown to red-orange.

Digestive system

Near the mouth and surrounding the outer lips of the buccal mass is a narrow ring of small, simple oral glands. The buccal mass (Fig. 12A) is somewhat dorsoventrally compressed, muscular, with a circular opening. The paired salivary glands are very thin anteriorly and expand posteriorly into the dendritic, glandular portion with numerous ramifications. The oesophagus is a straight glandular tube which expands into the corrugated, saccate stomach. From the stomach arise three major branches of the digestive gland: two branches emanate from the anterodorsal portion of the stomach and give rise to the left and right anterior digestive branches; the third branch arises at the ventral portion of the stomach and branches to the right and left posterior digestive branches. The intestine emerges from the posterior portion of the stomach and curves to the right, continuing posteriorly to the anus. The anus is surrounded by a large anal gland.

The jaws (Figs 12B, 13A) are of moderate thickness, angular and terminate posteriorly in a rather acute point. The masticatory border consists of 7 or 8 large, rounded denticles. The radula (Figs 13B, 14) is broad, consisting of 18 to 23 rows of teeth. There are 19 to 26 gradually arched, edenticulate lateral teeth on each side of the somewhat broad rachidian tooth. In the ten specimens examined, the rachidian teeth all possess 6 to 10 minute striations on each side of the base of the elongate central cusp. The lateral teeth have an elongate cusp

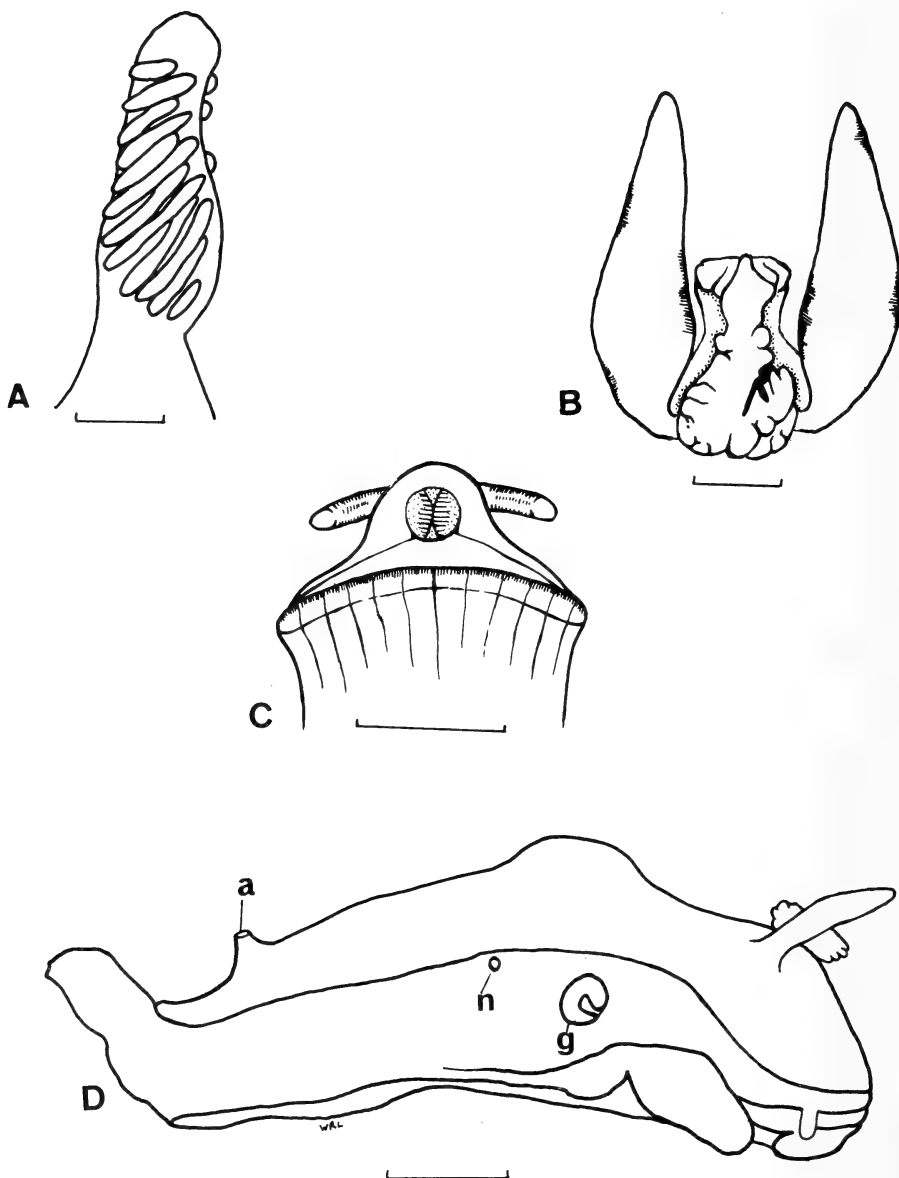


Fig. 10. *Janolus longidentatus* sp. nov. A. Rhinophore, scale 0,5 mm. B. Inter-rhinophoral crest, scale 0,5 mm. C. Ventral view of head, scale 1,5 mm. D. Lateral view, scale 2,0 mm. Figs 2A-B, D are drawn from preserved material, Fig. 2C is from living material.

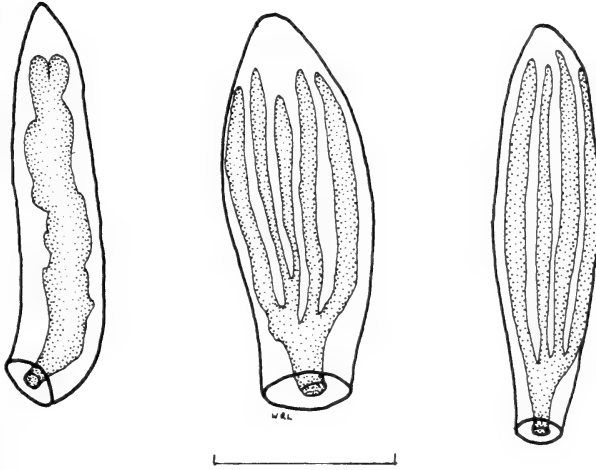


Fig. 11. *Janolus longidentatus* sp. nov.
Cerata dissected to show branching of digestive gland.
Scale 1,0 mm.

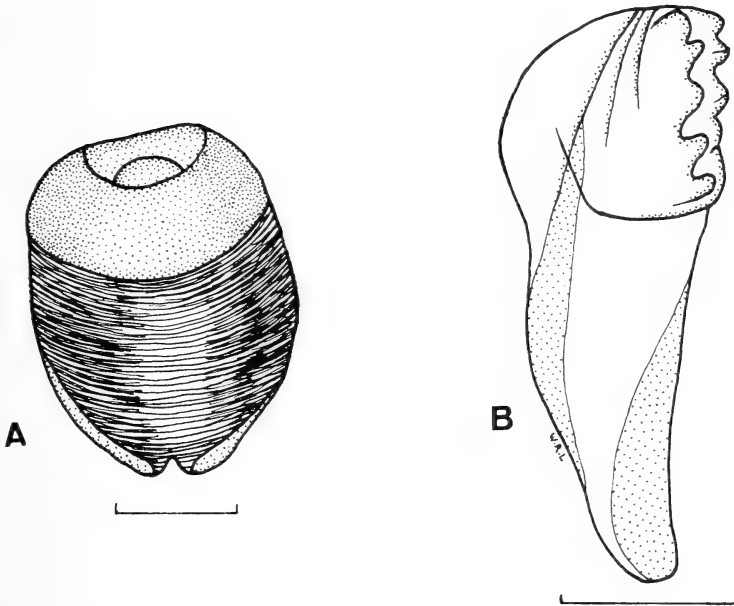


Fig. 12. *Janolus longidentatus* sp. nov.
A. Buccal mass, scale 1,0 mm.
B. Jaw, scale 1,0 mm.

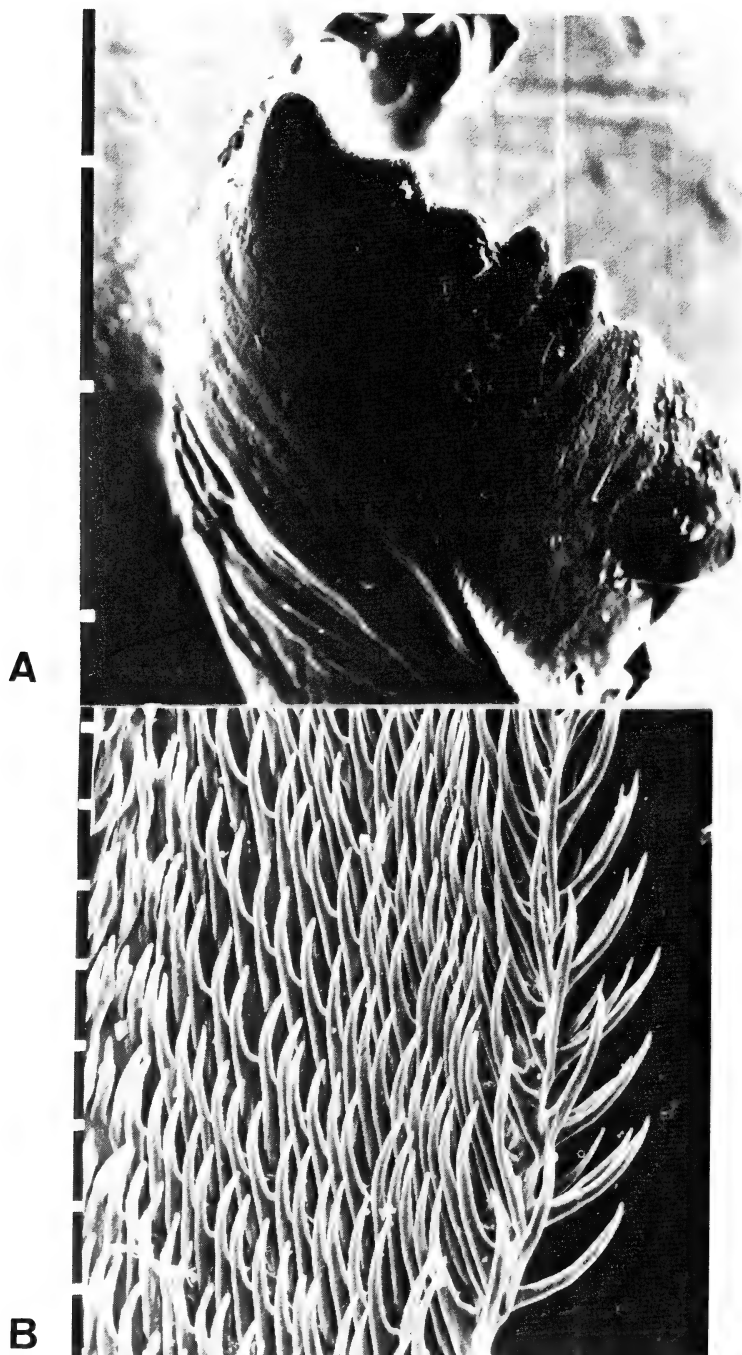


Fig. 13. *Janolus longidentatus* sp. nov. A. Scanning electron micrograph of masticatory border of jaw, scale $300\ \mu\text{m}$ between squares. B. Scanning electron micrograph of radula, scale $10\ \mu\text{m}$ between squares.

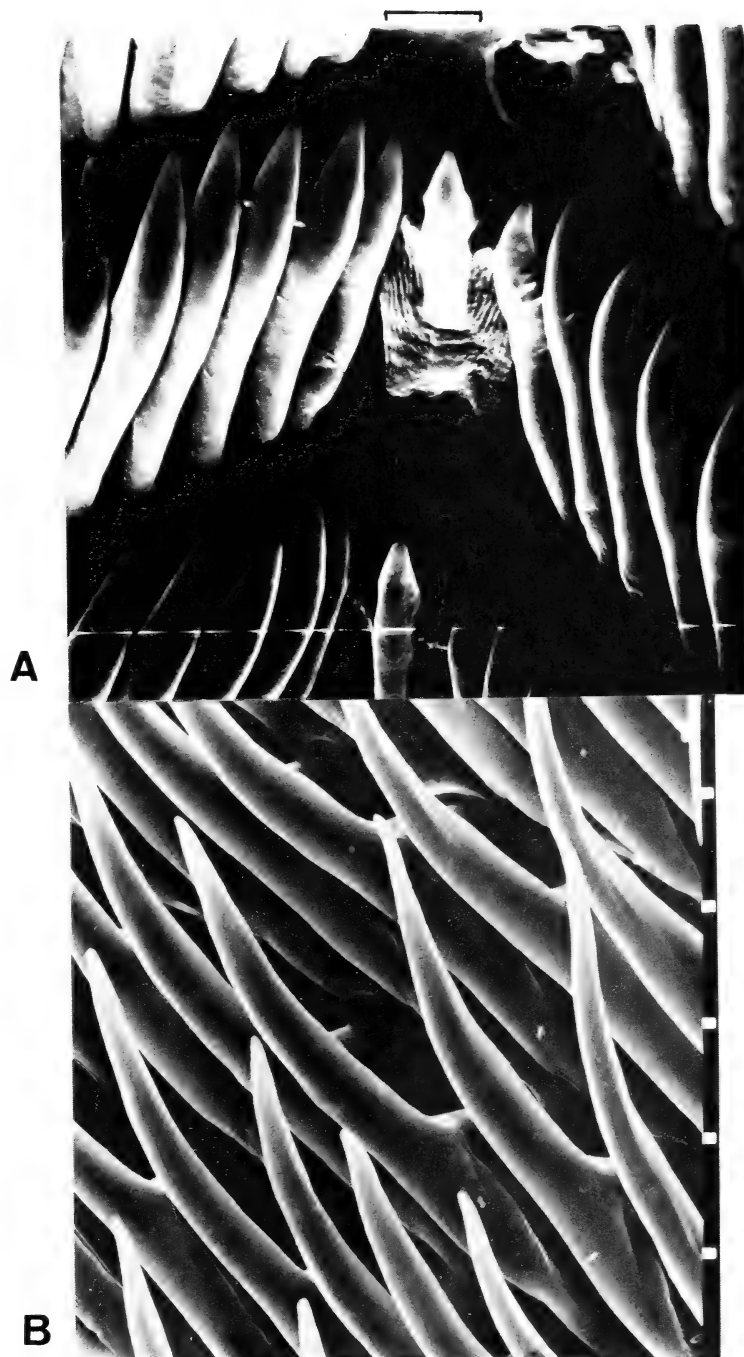


Fig. 14. *Janolus longidentatus* sp. nov. A. Scanning electron micrograph of central portion of radula, scale 30 μm . B. Scanning electron micrograph of lateral teeth from outer portion of radula, scale 30 μm between squares.

and increase in length towards the outer edges of the radula. Only the outermost teeth decrease in length.

Central nervous system (Fig. 15)

The major ganglia are situated in the circumoesophageal nerve ring. The cerebral and pleural ganglia are largely distinct. The anteriormost nerve of the dorsal surface of the cerebral ganglia bifurcates near its base with the inner branch innervating the inter-rhinophoral crest and the outer branch innervating the rhinophores. There is a distinct rhinophoral ganglion near the apex of the rhinophoral nerve. The eyes are situated at the apex of short optic nerves which join the central nervous system via small optic ganglia at the junction of the cerebral and pleural ganglia. Extending from the cerebral ganglia are the buccal nerves which join the round buccal ganglia. Anterior to each buccal ganglion is a minute gastro-oesophageal ganglion. The pedal ganglia are long with an elongate commissure between them.

Reproductive system (Fig. 16)

The follicles of the ovotestis are numerous and arranged into distinct lobes. The thick ampulla has 2 or 3 convolutions and narrows to the bifurcation of the vas deferens and oviduct. The glandular prostatic vas deferens is short with few convolutions. It enlarges into a much thicker penis sac which is recurved to an acutely pointed unarmed penial papilla. The muscular oviduct is embedded

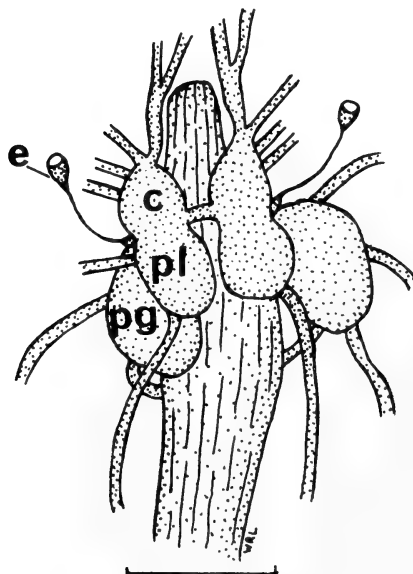


Fig. 15. *Janolus longidentatus* sp. nov.
Central nervous system.
Scale 1,0 mm.

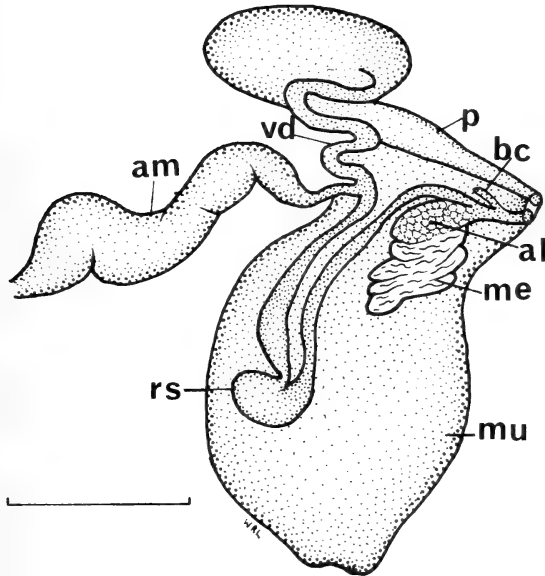


Fig. 16. *Janolus longidentatus* sp. nov.
Reproductive system.
Scale 1,0 mm.

between two lobes of the mucous gland and branches near the middle of its length to a short, bulbous receptaculum seminis. The major branch continues distally to its connection with the albumen gland and female gonopore. The narrow, linear bursa copulatrix joins the oviduct near the junction of the female gland mass, at the female atrium.

Egg mass (Fig. 17)

The egg mass is a low, flat spiral consisting of 3 or 4 whorls and corresponds to type B (Hurst 1967). There are 5 to 9 eggs per capsule.

Natural history

Janolus longidentatus feeds upon the cheilostomatous ectoproct *Menipea triseriata* Busk. It is commonly found in False Bay but has not been encountered on the Atlantic coast of the Cape Peninsula. *J. longidentatus* appears to have a seasonal distribution. Specimens have not been found from February to July and appear to be present largely in the winter and spring months. Specimens have been found from the intertidal to 30 m depth.

Bonisa gen. nov.

Diagnosis

Body stout, ovoid in outline. Rhinophores perfoliate. Inter-rhinophoral crest low, triangular with few convolutions. Cerata smooth, caducous, not

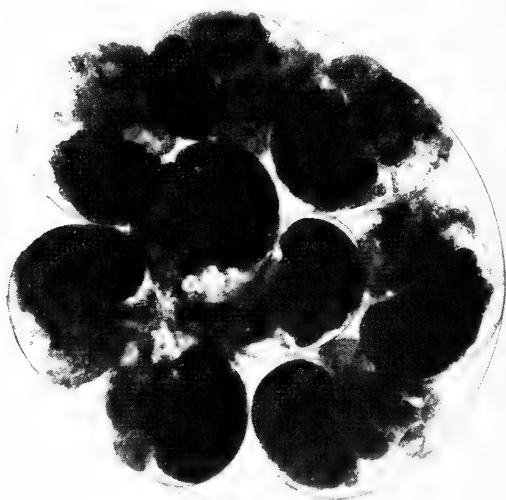
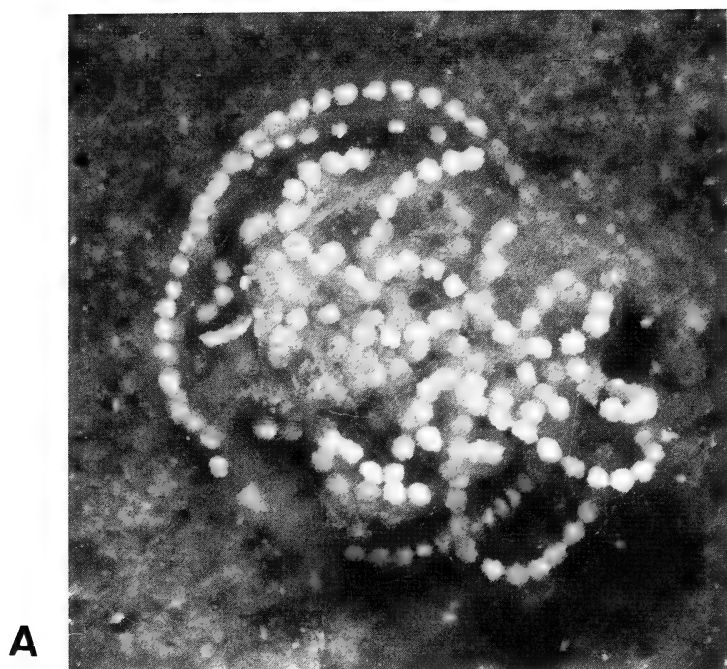


Fig. 17. *Janolus longidentatus* sp. nov.

A. Egg mass $\times 6$.

B. Single egg capsule $\times 100$.

containing branches of digestive gland. Gonopore near middle of body with nephroproct in posterior third of body. Oral glands small, simple. Salivary glands well developed with basal bulb. Digestive gland of three lobes surrounding stomach, not extending into notum or cerata. Anal glands absent. Jaws thick with smooth masticatory border. Rachidian and lateral teeth weakly to strongly denticulate. Pedal ganglia lateral to well separated cerebral and pleural ganglia. Optic nerves elongate. Reproductive system hermaphroditic, androdiaulic. Vas deferens short, prostatic, expanding into blunt, corrugated penis. Receptaculum seminis large, muscular and adjacent to gonopore. Bursa copulatrix small, linear and joining receptaculum seminis at female gonopore.

Type species

Bonisa nakaza sp. nov.

Etymology

Bonisa is named for my wife Bonnie Isabel Julien Gosliner.

Bonisa nakaza sp. nov.

Figs 1D–F, 18–25

Type material

Holotype—SAM–A34886, 20 m depth, off Llandudno (34°01'S 18°20'E), 23 December 1979.

Paratypes—SAM–A34887, 4 whole specimens, 20 m depth, off Llandudno (34°01'S 18°20'E), 23 December 1979

Other material

1 specimen, 10 m depth, Oudekraal (33°59'S 18°21'E), 13 January 1980

2 specimens, 10 m depth, Castle Rocks, False Bay (34°18'S 18°29'E), 17 January 1980

Etymology

Nakaza is a Zulu word meaning 'to adorn with beautiful colours', and the name is based on the bright coloration typical of this species.

External morphology

Fully mature specimens may reach a length of 100 mm. The body is broad, roughly oval in outline. The rhinophores (Fig. 18A) are perfoliate with 14 to 23 transverse lamellae. The slightly convoluted inter-rhinophoral crest (Fig. 18B) is triangular in shape, widest anteriorly. The mid-dorsal anus is located near the posterior end of the notum. The broad head (Fig. 18C) is round in shape, with a secondary, anterior lobe. The paired oral tentacles are moderately elongate and situated on either side of the head. The foot is transversely grooved at its

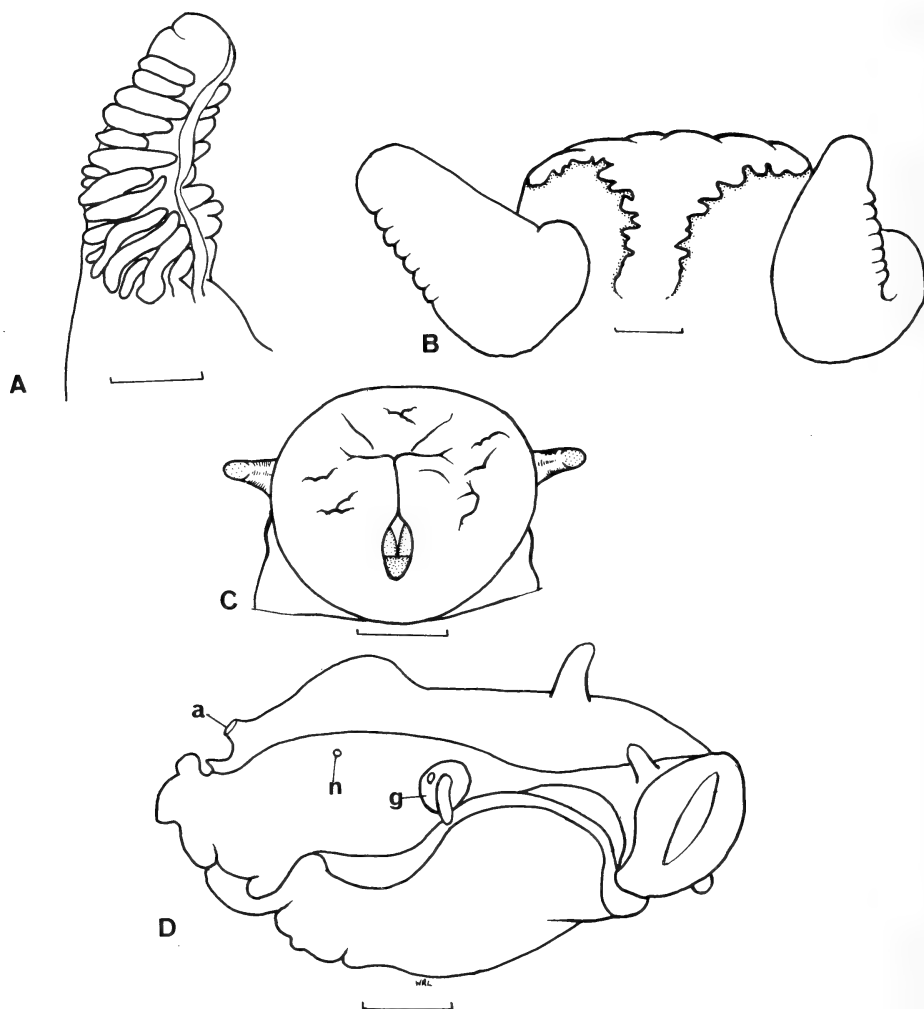


Fig. 18. *Bonisa nakaza* gen. et. sp. nov. A. Rhinophore, scale 1,0 mm. B. Inter-rhinophoral crest, scale 1,0 mm. C. Ventral view of head, scale 1,0 mm. D. Lateral view, scale 5,0 mm.

Figs 2A-B, D are drawn from preserved material, Fig. 2C is from living material.

anterior limit. The separate male and female gonopores are located near the middle of the right side of the body (Fig. 18D). The nephroproct is situated more posteriorly, in the posterior third of the animal. The elongate, readily caducous cerata are smooth and cylindrical. They are arranged in 16 to 21 diagonal rows per side with 8 to 10 cerata per row. Within the cerata a central muscular duct is present but this contains no extension of the digestive gland. At the base of each ceras is a ganglion which bifurcates into two nerves which extend distally into the ceras (Fig. 19A).

The living animals are variably and brightly coloured. (Fig. 1D-F). The general body colour ranges from translucent white to yellow or yellow-orange. Yellow or orange pigment is particularly concentrated on the anterodorsal surface. The rhinophores possess varying amounts of yellow or orange pigment. The cerata are strikingly variable in their coloration. On the surface they are most commonly yellow, basally, with varying amounts and shades of blue pigment on the more distal portion. Some specimens possess a small subapical concentration of black or dark-blue pigment within the ceratal ducts. Other

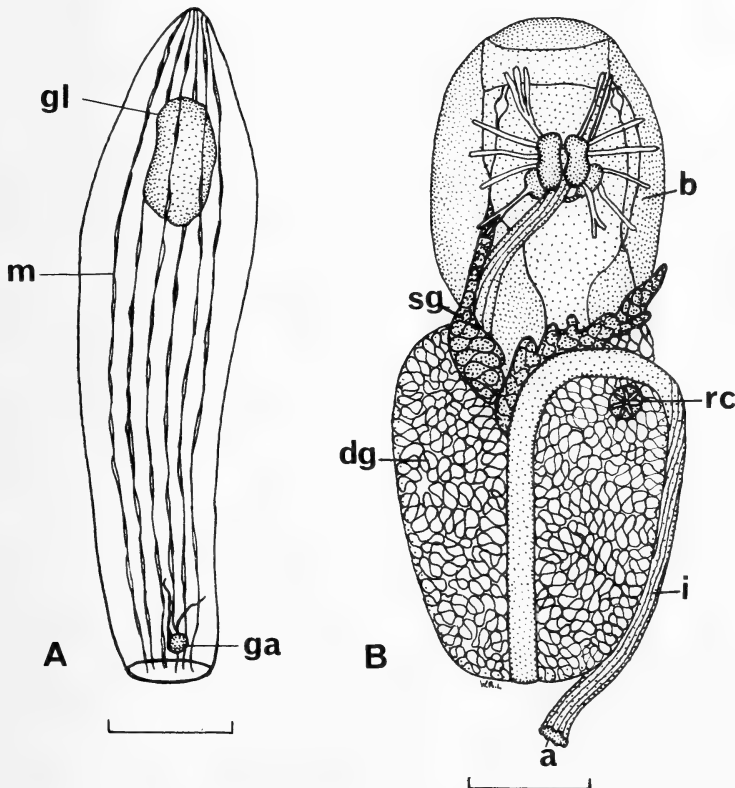


Fig. 19. *Bonisa nakaza* gen. et sp. nov.

A. Ceras, scale 1,0 mm.

B. Digestive system, scale 2,0 mm.

specimens, which entirely lack blue or yellow pigment, possess only an apical band of orange on each ceras and rhinophore. A few juvenile specimens have cerata which are pinkish with blue pigment and opaque white apices. Since adult specimens of different colour patterns have been observed copulating, they are considered to be conspecific.

Digestive system (Fig. 19B)

There is a moderately large ring of oral glands surrounding the outer lips. The massive buccal mass is highly muscular and occupies the anterior third of the body cavity. The paired salivary glands are well developed, extending from the posterior limit of the oesophagus. Near their origin there is a large, spherical expansion of the salivary gland duct which probably functions as a vestibule for storage of secretory products. The oesophagus is short and expands into a thin-walled stomach. On the dorsal surface of the stomach is a large corrugated portion. Surrounding the stomach are three major lobes of the highly dendritic digestive gland. A digestive lobe joins the stomach on both the anterolateral sides of the stomach with a third lobe connecting to the antero-ventral portion. The intestine emerges from the posteroventral portion of the stomach and continues posteriorly to the anus. The anus is not surrounded by anal glands.

The buccal mass (Fig. 20A) has an oblong opening. The jaws (Fig. 20B) are thick and broad with a smooth masticatory border (Fig. 21) which is supported by an elevated arch of chitin. The outer borders of the jaws are sharply indented. The radula (Fig. 22) contains 21 to 46 rows of teeth with 7 to

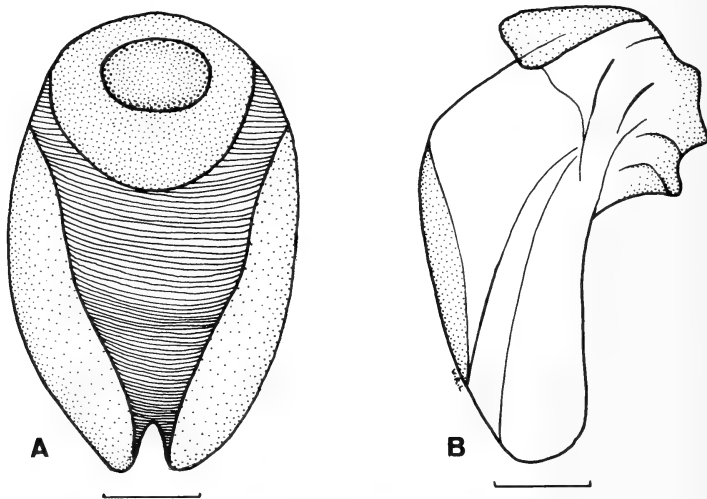


Fig. 20. *Bonisa nakaza* gen. et sp. nov.

A. Buccal mass, scale 1,0 mm.

B. Jaw, scale 1,0 mm.



Fig. 21. *Bonisa nakaza* gen. et sp. nov. Scanning electron micrograph of masticatory border of jaw. Scale 100 μm between squares.

33 laterals on each side of the rachidian teeth. The rachidians possess 2 to 5 small or elongate denticles. The lateral teeth possess 2 to 7 denticles on each side of the elongate central cusp.

Central nervous system (Fig. 23)

The major ganglia of the central nervous system are situated in the circumoesophageal nerve ring. The cerebral ganglia are closely appressed to each other without a distinct commissure and are joined posteriorly by the distinct pleural ganglia. The anteriormost dorsal nerve of the cerebral ganglion innervates the rhinophores and divides near the middle of its length to give rise to a very thin branch which innervates the inter-rhinophoral crest. The eyes are situated at the distal end of the elongate optic nerve which joins the junction of the cerebral and pleural ganglia via a short optic ganglion. Extending anteriorly from the cerebral ganglia are the paired buccal nerves which enlarge into the buccal ganglia on the surface of the buccal mass. Ventral to the oesophagus, the buccal ganglia are joined by a commissure of moderate length and anteriorly each gives rise to a small gastro-intestinal ganglion. The pedal ganglia are situated laterally to the cerebral and pleural ganglia rather than posteriorly, and are connected by an elongate commissure.

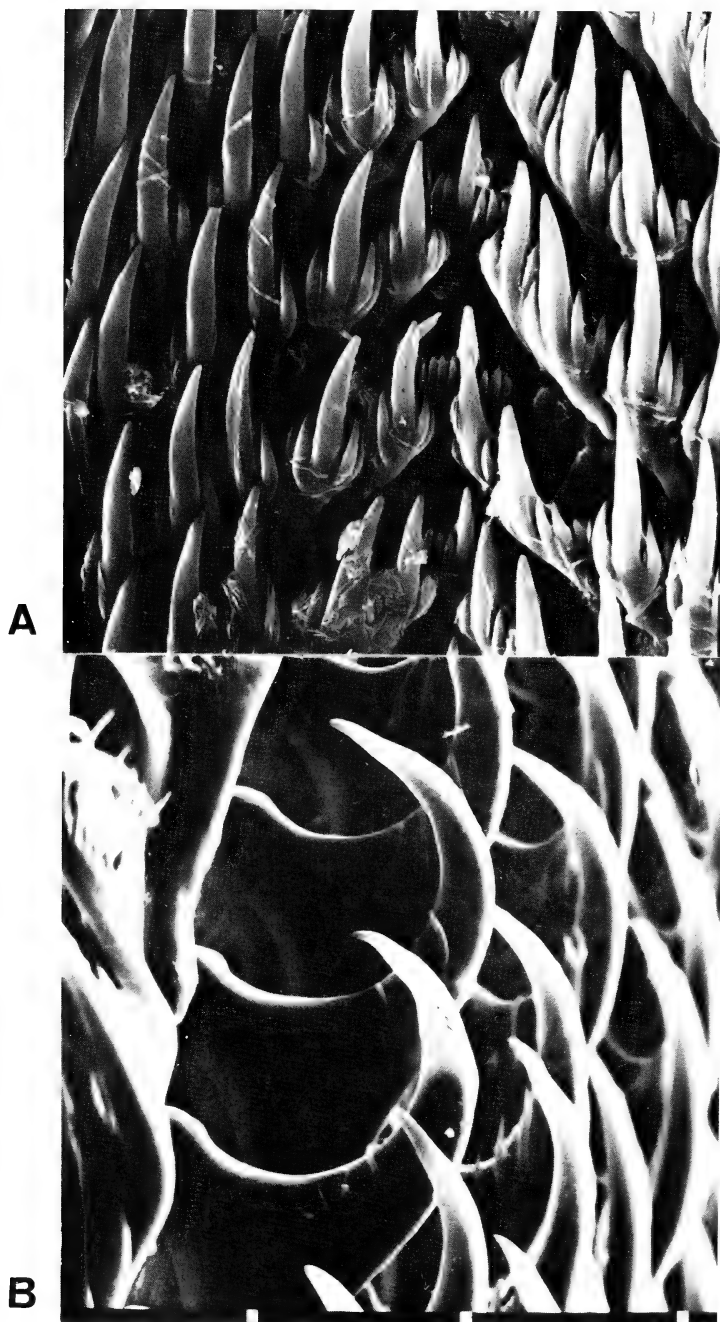


Fig. 22. *Bonisa nakaza* gen. et sp. nov. A. Scanning electron micrograph of central portion of radula. B. Scanning electron micrograph of lateral teeth from outer portion of radula. Scales 30 μm between squares.

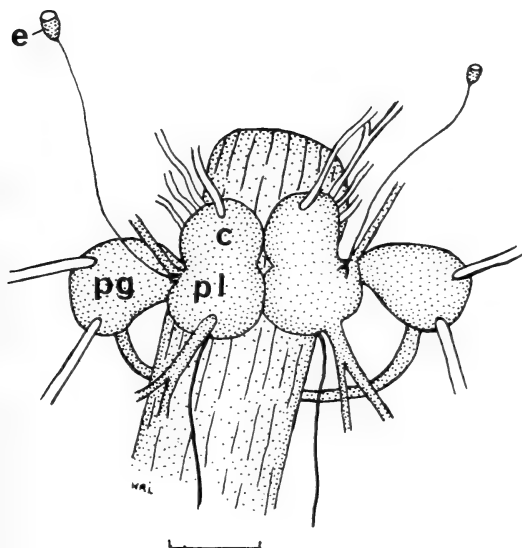


Fig. 23. *Bonisa nakaza* gen. et sp. nov.
Central nervous system.
Scale 0,5 mm.

Reproductive system (Fig. 24)

The ovotestis consists of numerous follicles which are united into an ovoid mass. The preampullary duct emerges from the anterior end of the ovotestis and expands into a highly convoluted, thickened ampulla. The ampulla narrows anteriorly and divides into the oviduct and vas deferens. The vas deferens is short, thick, and muscular, and expands into the massive penis sac. The penial papilla is club-shaped and strongly corrugated. The oviduct is muscular and joins the large receptaculum seminis near its base. Traversing the base of the receptaculum seminis is a small, linear bursa copulatrix which joins the receptaculum near the female gonopore. At the base of the receptaculum sac is a thick duct which connects it with the small albumen and membrane portions of the female gland mass. These glands join the massive mucous gland, which forms the bulk of the female gland mass.

Egg mass (Fig. 25)

The egg mass is about 20 to 30 mm high, consists of numerous convolutions and corresponds to type B (Hurst 1967). There are one or two eggs per capsule. The egg mass is frequently deposited on the finger-like projections of gorgonians.

Natural history

Bonisa nakaza is found in the shallow subtidal, at depths of 3 to 30 m on both the Atlantic and Indian Ocean coasts of the Cape Peninsula. It is

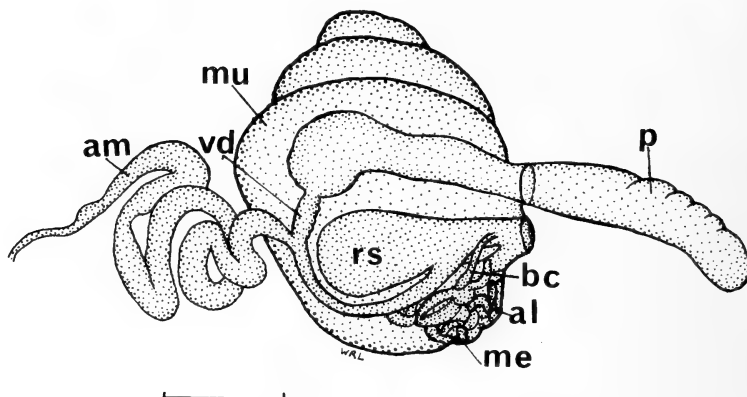


Fig. 24. *Bonisa nakaza* gen. et sp. nov.
Reproductive system.
Scale 4,0 mm.

associated with and feeds upon the heavily calcified arborescent cheilostomatous ectoproct, *Tubucellaria levinseni* Canu & Bassler, 1930.

DISCUSSION OF THE JANOLIDAE

Within the suborder Arminacea, the tribe Pachygnatha is subdivided into three families, the Madrellidae, Dironidae, and Janolidae (Franc 1968). The Janolidae have been separated from the other two families by having a broad rather than narrow radula, a medial rather than lateral anus, and by having extensions of the digestive gland into the cerata. With the discovery of *Bonisa nakaza* in this study, the diagnosis of the Janolidae must be expanded to include forms with or without extensions of the digestive gland into the cerata.

The family Janolidae has been previously subdivided into five genera. *Proctonotus* Alder & Hancock, 1844, and *Caldukia* Burn & Miller, 1969, lack an inter-rhinophoral crest. *Caldukia* can be separated from *Proctonotus* by its distinctively stout rhinophores with transverse lamellae and its significantly narrower radular ribbon. Of the genera which possess an inter-rhinophoral crest *Galeojanolus* Miller, 1971, can be separated from *Janolus* Bergh, 1884, and *Antiopella* Hoyle, 1902, by the helmet-like appendage extending anteriorly from the head. *Bonisa* gen. nov. must be added to this group and can be readily separated from the other janolids by the fact that the digestive gland surrounds the stomach rather than entering the notum and cerata. In several respects *Bonisa nakaza* most closely approaches *Galeojanolus ionnae* Miller, 1971. Both species have an ovoid body shape, similar coloration, perfoliate rhinophores, a low, broad inter-rhinophoral crest with few convolutions, jaws with a smooth masticatory border, a moderately broad radula with strongly denticulate teeth and a diaulic reproductive system. Both species lack anal glands. However, there are several significant differences which distinguish the species. *Galeo-*

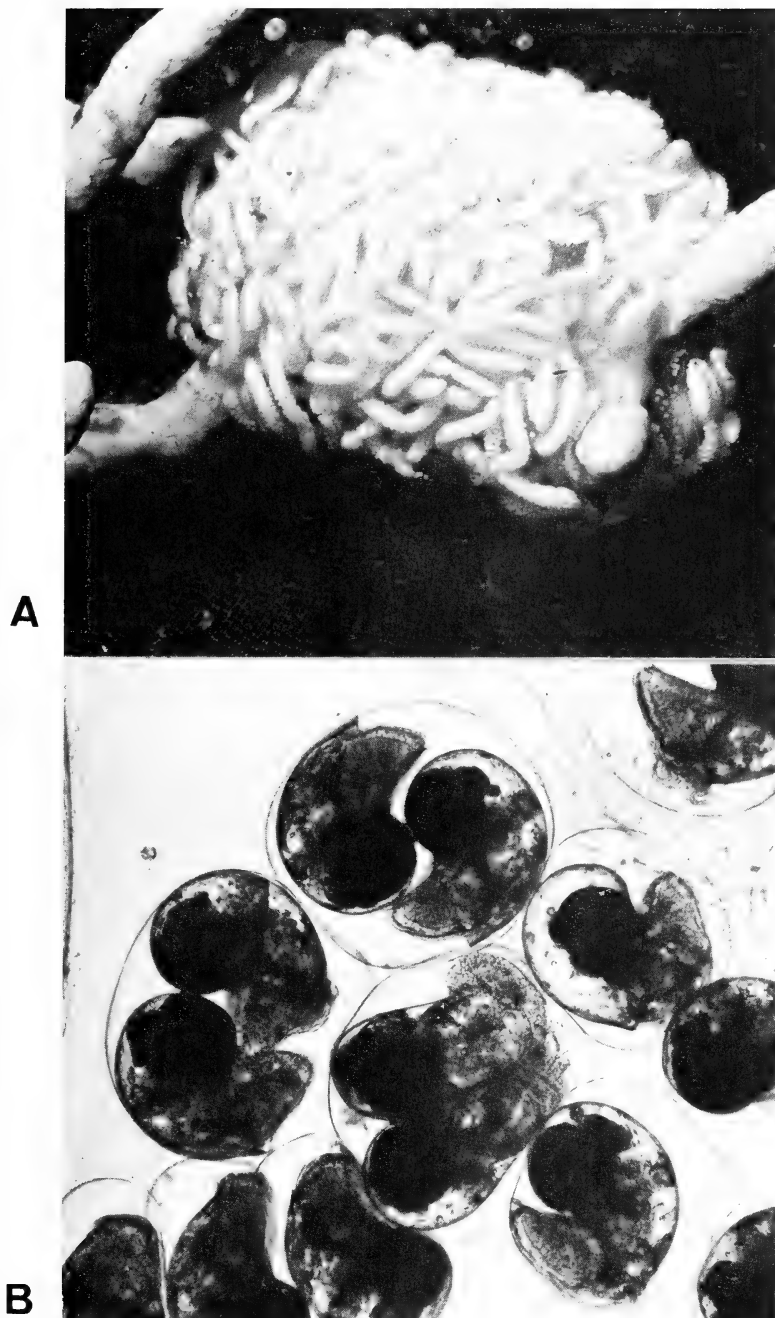


Fig. 25. *Bonisa nakaza* gen. et sp. nov.

A. Egg mass $\times 3$.

B. Several egg capsules $\times 100$.

janolus ionnae possesses an elongate helmet-like appendage on the anterior end of the head which may be used in capturing mobile prey (Miller 1971), while there is a short lobe anterior to the head of *Bonisa nakaza*. *G. ionnae* has papillate, inflated cerata, while they are smooth and cylindrical in *B. nakaza*. *B. nakaza* lacks complex oral glands and is devoid of digestive gland ducts in the cerata which are both present in *G. ionnae*. The reproductive system of *G. ionnae*, while not fully mature, has a conical, tapered penis and an elongate vas deferens, while *B. nakaza* has a short vas deferens and a blunt, corrugated penis similar in shape to that described for *Janolus cristatus* (Schmekel 1970). Miller described a bursa copulatrix in *G. ionnae*, while *B. nakaza* possesses both a large receptaculum seminis and a small bursa copulatrix situated near the gonopore. These differences, particularly those of the digestive system, warrant generic as well as specific separation.

It is difficult to separate *Antiopella* and *Janolus*. Several authors have united the genera (Thiele 1931; Franc 1968; Thompson & Brown 1976), while others have maintained them as distinct (Eliot 1906; Pruvot-Fol 1954; Marcus 1958; Burn & Miller 1969; Baba & Abe 1970; Miller 1971). Pruvot-Fol (1954) stated that *Antiopella* may be separated from *Janolus* by virtue of the fact that the component species possess a denticulate instead of smooth masticatory border of the jaw, smooth instead of papillate cerata, and branched instead of undivided ducts of the digestive gland within the cerata. However, several species of janolids (Table 1) possess intermediate or variable character states or individual characters. They may also possess a mixture of 'Antiopella' and 'Janolus' characters. Marcus (1958: 40) noted that the structure of the cerata in the type species of *Janolus*, *J. australis*, is questionable. Several workers who have suggested the separation of *Antiopella* from *Janolus* have stated that jaw denticulation alone should not warrant generic separation (Pruvot-Fol 1954; Marcus 1958). The fact that *Janolus capensis* and *J. longidentatus* are very similar in many aspects of their external and internal anatomy (present study) but differ in jaw denticulation supports the view that this character alone should not be utilized for generic separation in the Janolidae. The division of the genital ducts into a diaulic or triaulic configuration varies significantly within *Janolus* and *Antiopella*. The reproductive anatomy is described for eight of the fifteen species described in both genera. In three species, *A. mucloc* (Marcus 1958), *Janolus comis* (Marcus 1958), and *J. toyamensis* (present

TABLE 1
Antiopella and *Janolus* characteristics in three species of janolids.

Species	Ceratal epithelium	Ceratal ducts	Jaws
<i>Janolus toyamensis</i>	smooth or with few tubercles (A or I)	branched (A)	large denticles (I)
<i>Janolus capensis</i>	smooth (A)	branched (A)	smooth (J)
<i>Janolus fuscus</i>	smooth (A)	branched (J)	denticulate (A)
A— <i>Antiopella</i>	I—Intermediate	J— <i>Janolus</i>	

study), the reproductive system is triaulic. In *A. cristata* (Schmekel 1970), *J. hyalinus* (Schmekel 1970), *J. fuscus* (present study), *J. capensis* (present study), and *J. longidentatus* (present study) a diaulic configuration is present. The reproductive system of the type species of *Janolus*, *J. australis*, is incompletely described. There is no correlation between division of the genital ducts and jaw denticulation. There is, therefore, little basis for separating *Antiopella* Hoyle, 1902, from *Janolus* Bergh, 1884, and *Antiopella* is here regarded as a junior subjective synonym of *Janolus* on the basis of priority.

KEY TO THE GENERA OF THE JANOLIDAE

- | | | |
|---|---|---------------------|
| 1 | Digestive gland surrounding stomach | <i>Bonisa</i> |
| | Digestive gland extending into notum and cerata | 2 |
| 2 | Inter-rhinophoral crest present | 3 |
| | Inter-rhinophoral crest absent | 4 |
| 3 | Head with helmet-like extension | <i>Galeojanolus</i> |
| | Head without extension | <i>Janolus</i> |
| 4 | Rhinophoral club stout with transverse lamellae, radula 6.1.6 | <i>Caldukia</i> |
| | Rhinophores with inconspicuous lamellae, radula broad | <i>Proctonotus</i> |

The following species are considered to constitute the family Janolidae (*indicates type species):

Bonisa gen. nov.

1. **Bonisa nakaza* sp. nov.

Caldukia Burn & Miller, 1969

2. **Caldukia affinis* (Burn, 1958)

Proctonotus? affinis Burn, 1958: 32, fig. 8, pl. 7 (fig. 15).

Caldukia affinis (Burn, 1958), Burn and Miller, 1969: 23, figs 1–2, pl. 2.

3. *Caldukia albolineata* Miller, 1970

Caldukia albolineata Miller, 1970: 279, figs 1–10.

4. *Caldukia rubiginosa* Miller, 1970

Caldukia rubiginosa Miller, 1970: figs 11–21.

Galeojanolus Miller, 1971

5. **Galeojanolus ionnae* Miller, 1971

Galeojanolus ionnae Miller, 1971: 491, figs 1–4.

Janolus Bergh, 1884

6. **Janolus australis* Bergh, 1884

Janolus australis Bergh, 1884: 19, pl. 8 (figs 15–22), pl. 9 (figs 6–8).

7. *Janolus barbarensis* (Cooper, 1863)

Aeolis barbarensis Cooper, 1863: 59.

Janolus coeruleopictus Cockerell & Eliot, 1905: 48, pl. 8 (figs 12–16). O'Donoghue, 1922: 141.

Janolus barbarensis (Cooper, 1863), O'Donoghue, 1922: 141.

Antiopella aureocincta MacFarland, 1966: 303, pl. 57 (figs 1–5), pl. 63 (figs 13–30), pl. 64 (figs 11–17). Roller, 1970: 372, in part.

8. *Janolus capensis* Bergh, 1907

Janolus capensis Bergh, 1907: 90, pl. 7 (figs 6–21).

9. *Janolus comis* Marcus, 1955

Janolus comis Marcus, 1955: 170, pl. 25 (figs 226–236).

10. *Janolus cristatus* (Chiaje, 1841)

Eolis cristatus Chiaje, 1841: pl. 88 (figs 1–12).

Janus spinolae Verany, 1845: 24, pl. 2 (fig. 9). Pruvot-Fol, 1954: 375.

Antiopa splendida Alder & Hancock, 1848: 190. Alder & Hancock, 1851.

Antiopella cristata (Chiaje, 1841), Hoyle, 1902: 214.

Janolus cristatus (Chiaje, 1841), O'Donoghue, 1924: 1.

11. *Janolus flagellatus* Eliot, 1906

Janolus flagellatus Eliot, 1906: 374.

(Likely a junior synonym of *J. hyalinus* (Alder & Hancock, 1854). Eliot (1910) considered this as an uncertain species. It was distinguished from *J. hyalinus* by possession of a flagellar penis which has subsequently been described in *J. hyalinus* (Schmekel 1970).)

12. *Janolus fuscus* O'Donoghue, 1924

Janolus fuscus O'Donoghue, 1924: 16, pl. 2 (figs 18–20).

Antiopella aureocincta Johnson & Snook, 1927: 500. Nomen nudum, Steinberg, 1963: 66.

Antiopella aureotincta MacGinitie & MacGinitie, 1949: 135. Nomen nudum, Steinberg, 1963: 66.

Antiopella aureocincta MacFarland, 1966: 303, pl. 57 (figs 1–5), pl. 63 (figs 13–30), pl. 64 (figs 11–17). Roller, 1970: 372, in part.

13. *Janolus hyalinus* (Alder & Hancock, 1854)

Antiopa hyalina Alder & Hancock, 1854a: 105.

Janolus hyalinus (Alder & Hancock, 1854), Eliot, 1906: 374.

14. *Janolus indicus* (Eliot, 1909)

Antiopella indica Eliot, 1909: 143.

Janolus indicus (Eliot, 1909), **comb. nov.**

15. *Janolus longidentatus* **sp. nov.**16. *Janolus mirabilis* Baba & Abe, 1970

Janolus mirabilis Baba & Abe, 1970: 65, figs 2–3.

17. *Janolus mucloc* (Marcus, 1958)

Antiopella mucloc Marcus, 1958: 37, figs 62–71.

Janolus mucloc (Marcus, 1958), **comb. nov.**

18. *Janolus novozealandicus* (Eliot, 1907)

Antiopella novozealandica Eliot, 1907: 331.

Janolus novozealandicus (Eliot, 1907), **comb. nov.**

19. *Janolus praeclarus* (Bouchet, 1975)

Antiopella praeclara Bouchet, 1975: 127, pl. 1 (fig. 3), fig. 5.

Janolus praeclarus (Bouchet, 1975), **comb. nov.**

20. *Janolus toyamensis* Baba & Abe, 1970

Janolus toyamensis Baba & Abe, 1970: 63, fig. 1.

Proctonotus Alder & Hancock, 184421. **Proctonotus mucroniferus* (Alder & Hancock, 1844)

Venilia mucronifera Alder & Hancock, 1844: 163, pl. 2.

Proctonotus mucroniferus (Alder & Hancock, 1844) Alder, 1844: 407.

Zephyrina pilosa Quatrefages, 1844: 130, pl. 3 (fig. 1), pl. 4 (fig. 1), pl. 5 (figs 1–2), pl. 6 (figs 1, 11–12). Pruvot-Fol, 1954: 372.

Morphological variability

Janolus varies in its external and internal morphology. The major morphological features and their character states in the fifteen described species of *Janolus* are summarized in Table 2. Many taxa are incompletely described, including the type species, but the available morphological data does permit a review of the variability within the genus. All described species have a simply rounded head, perfoliate or, exceptionally, papillate (*J. comis* Marcus, 1955) rhinophores, an inter-rhinophoral crest, and cerata which contain ducts of the digestive gland. The inter-rhinophoral crest may be small and rectangular or may be highly elaborate as in *J. cristatus* (Alder & Hancock 1854b), *J. capensis* (present study), *J. novozealandicus* (Eliot 1907), and *J. longidentatus* (present study). The cerata are papillate in *J. comis* (Marcus 1955), *J. hyalinus* (Alder & Hancock 1854b), and *J. mirabilis* (Baba & Abe 1970), and smooth in the remainder of the species. The cerata of *J. toyamensis* are variable, with scattered, small papillae (Baba & Abe 1970) or with an entirely smooth surface (present study). The digestive gland may extend only within the basal half of the cerata in *Janolus comis* (Marcus 1958), *J. hyalinus* (Bergh 1904), and *Galeojanolus ionnae* (Miller 1971), or extend to the apex of the cerata in the remaining species of *Janolus*. Within the cerata the digestive gland may be branched or unbranched. In species with a branched digestive gland, the splitting may occur apically in *J. cristatus* (Alder & Hancock 1854b) and *J. barbarensis* (MacFarland 1966), near the middle in *J. mucloc* (Marcus 1958), *J. praeclarus* (Bouchet 1975), *J. toyamensis* (Baba & Abe 1970), and *J. capensis* (present study), or basally in *J. longidentatus* (present study). In most species of *Janolus* all cerata contain extensions of digestive gland except *J. hyalinus* (Eliot 1910), *J. comis* (Marcus 1958), *J. capensis* (present study), and *J. longidentatus* (present study) where the anteriormost cerata are devoid of digestive gland tissue.

It appears that in all species of *Janolus* that have been studied, simple oral glands and elaborate salivary glands are present and the digestive gland occurs as three major branches from the stomach. Anal glands appear to be present in all species except *J. comis* (Marcus 1955) and *J. fuscus* (present study).

TABLE 2
Comparative morphology of *Janolus*.

<i>Species of Janolus</i>	<i>Colour</i>	<i>Ceratal epithelium</i>	<i>Ceratal ducts</i>	<i>Jaws</i>	<i>Radular teeth</i>
<i>J. australis</i> . .	unknown	smooth ?	unknown	smooth	rachidian and laterals smooth
<i>J. barbarendis</i> . .	translucent white; cerata with gold and blue	smooth	branched	unknown	rachidian smooth, laterals: inner 2 denticulate, outer smooth
<i>J. comis</i> . . .	light brown with dark-brown stipples	papillate	unbranched	smooth	rachidian denticulate, laterals: denticulate, variable
<i>J. cristatus</i> . .	cream or brown with opaque white cerata	smooth	branched at apex	8-12 denticles	rachidian and laterals smooth, rarely denticulate
<i>J. flagellatus</i> . .	unknown	unknown	unknown	smooth	rachidian and laterals smooth
<i>J. fuscus</i> . . .	translucent white with brown lines, cerata with yellow and white	smooth	unbranched	8-14 denticles	rachidian denticulate, laterals: inner 2 denticulate, outer smooth
<i>J. hyalinus</i> . .	cream with red-brown blotches; cerata dotted with white and brown	papillate	unbranched	smooth	rachidian and laterals smooth or finely denticulate
<i>J. indicus</i> . . .	translucent with red-brown spots, cerata grey-green	unknown	unknown	denticulate	rachidian and laterals smooth
<i>J. mirabilis</i> . .	yellow with brown and opaque white; cerata white at apex	papillate	unbranched ?	smooth	rachidian, denticulate, laterals: inner 2 denticulate, outer 2 smooth
<i>J. mucloc</i> . . .	transparent white with opaque white lines; cerata with orange spot and opaque white lines	smooth	branched, bifurcate below middle	8 denticles	rachidian denticulate, laterals: inner denticulate, outer smooth
<i>J. novozealandicus</i>	grey with purple stripe and spots; cerata with purple spots	smooth	unbranched	indistinct denticulation	rachidian and laterals smooth
<i>J. praeclarus</i> . .	orange with opaque white; cerata with yellow bands and bluish-white apex	smooth	branched	6 denticles	rachidian and laterals smooth
<i>J. toyamensis</i> . .	yellow with white and brown markings; cerata with yellow spot and red-brown apex	few minute papillae	branched	2 or 3 large denticles	rachidian and laterals smooth
<i>J. capensis</i> . .	translucent white with opaque white; cerata red-brown with opaque white apex	smooth	branched	smooth	rachidian and laterals smooth
<i>J. longidentatus</i> .	translucent white with opaque white; cerata red-brown with opaque white apex	smooth	branched basally	7-8 denticles	rachidian striate, laterals smooth

<i>Radular formula</i>	<i>Receptaculum seminis</i>	<i>Bursa copulatrix</i>	<i>Penis</i>	<i>Prostatic vas deferens</i>	<i>Reproductive ducts</i>	<i>References</i>
24 × 30–54.1.30–54	unknown	unknown	thicker than vas deferens	unknown	unknown	Bergh 1884
16 × 27.1.27	unknown	unknown	unknown	unknown	unknown	Cockerell & Eliot 1905 MacFarland 1966, in part
16 × 12–20.1.12–20 25 × 41.1.41	proximal, serial	absent	conical, flagellar	proximal to penis only	triaulic	Marcus 1955 Marcus 1958
30 × 40.1.40 24 × 33.1.33	proximal, semi-serial	minute, distal	blunt	throughout	diaulic	Alder & Hancock 1851 Alder & Hancock 1855 Schmekel 1970 Thompson & Brown 1976
15 × 20.1.20	unknown	large, elliptical	unknown	unknown	unknown	Eliot 1906
21 × 22.1.22 26 × 25.1.25	proximal, semi-serial	distal	conical	throughout	diaulic	O'Donoghue 1924 MacFarland 1966, in part present study
15 × 11–13.1.11–13	small, proximal, semi-serial	absent	elongate, flagellar	throughout	diaulic	Alder & Hancock 1854b Alder & Hancock 1855 Bergh 1888, Eliot 1906, Schmekel 1970
21 × 31.1.31	unknown	unknown	unknown	unknown	unknown	Eliot 1909
20 × 5.1.5	unknown	unknown	unknown	unknown	unknown	Baba & Abe 1970
18 × 24.1.24	proximal, semi-serial within female gland mass	absent	thick	throughout	triaulic	Marcus 1958
23 × 37.1.37	unknown	unknown	short	unknown	unknown	Eliot 1907
20 × 28.1.28	unknown	unknown	unknown	unknown	unknown	Bouchet 1975
20 × 10–20.1.10–20 19 × 25.1.25	proximal	absent	elongate, flagellar	throughout	triaulic	Baba & Abe 1970 present study
20 × 42.1.42 18 × 41.1.41 17 × 26.1.26	elongate, proximal, semi-serial	distal, minute	elongate, flagellar	throughout	diaulic	Bergh 1907 Barnard 1927 present study
18 × 21.1.21 22 × 26.1.26 20 × 20.1.20 21 × 21.1.21	short, proximal, semi-serial	distal, minute	conical	short	diaulic	present study

TABLE 2
Comparative morphology of *Janolus*.

Species of <i>Janolus</i>	Colour	Ceratal epithelium	Ceratal ducts	Jaws	Radular teeth
<i>J. australis</i>	unknown	smooth ?	unknown	smooth	rachidian and laterals smooth
<i>J. barbarensis</i>	translucent white; cerata with gold and blue	smooth	branched	unknown	rachidian smooth, laterals: inner 2 denticulate, outer smooth
<i>J. comis</i>	light brown with dark-brown stipples	papillate	unbranched	smooth	rachidian denticulate, laterals: denticulate, variable
<i>J. cristatus</i>	cream or brown with opaque white cerata	smooth	branched at apex	8-12 denticles	rachidian and laterals smooth, rarely denticulate
<i>J. flagellatus</i>	unknown	unknown	unknown	smooth	rachidian and laterals smooth
<i>J. fuscus</i>	translucent white with brown lines, cerata with yellow and white	smooth	unbranched	8-14 denticles	rachidian denticulate, laterals: inner 2 denticulate, outer smooth
<i>J. hyalinus</i>	cream with red-brown blotches; cerata dotted with white and brown	papillate	unbranched	smooth	rachidian and laterals smooth or finely denticulate
<i>J. indicus</i>	translucent with red-brown spots, cerata grey-green	unknown	unknown	denticulate	rachidian and laterals smooth
<i>J. mirabilis</i>	yellow with brown and opaque white; cerata white at apex	papillate	unbranched ?	smooth	rachidian, denticulate, laterals: inner 3 denticulate, outer 2 smooth
<i>J. mucloc</i>	transparent white with opaque white lines; cerata with orange spot and opaque white lines	smooth	branched, bifurcate below middle	8 denticles	rachidian denticulate, laterals: inner denticulate, outers smooth
<i>J. novozealandicus</i>	grey with purple stripe and spots; cerata with purple spots	smooth	unbranched	indistinct denticulation	rachidian and laterals smooth
<i>J. praeclarus</i>	orange with opaque white; cerata with yellow bands and bluish-white apex	smooth	branched	6 denticles	rachidian and laterals smooth
<i>J. toyamensis</i>	yellow with white and brown markings; cerata with yellow spot and red-brown apex	few minute papillae	branched	2 or 3 large denticles	rachidian and laterals smooth
<i>J. capensis</i>	translucent white with opaque white; cerata red-brown with opaque white apex	smooth	branched	smooth	rachidian and laterals smooth
<i>J. longidentatus</i>	translucent white with opaque white; cerata red-brown with opaque white apex	smooth	branched basally	7-8 denticles	rachidian striate, laterals smooth

Radular formula	Receptaculum seminis	Bursa copulatrix	Penis	Prostatic vas deferens	Reproductive ducts	References
24 × 30-54.1.30-54	unknown	unknown	thicker than vas deferens	unknown	unknown	Bergh 1884
16 × 27.1.27	unknown	unknown	unknown	unknown	unknown	Cockerell & Eliot 1905 MacFarland 1966, in part
16 × 12-20.1.12-20 25 × 41.1.41	proximal, serial	absent	conical, flagellar	proximal to penis only	trialucic	Marcus 1955 Marcus 1958
30 × 40.1.40 24 × 33.1.33	proximal, semi-serial	minute, distal	blunt	throughout	diaulic	Alder & Hancock 1851 Alder & Hancock 1855 Schmekel 1970 Thompson & Brown 1976
15 × 20.1.20	unknown	large, elliptical	unknown	unknown	unknown	Eliot 1906
21 × 22.1.22 26 × 25.1.25	proximal, semi-serial	distal	conical	throughout	diaulic	O'Donoghue 1924 MacFarland 1966, in part present study
15 × 11-13.1.11-13	small, proximal, semi-serial	absent	elongate, flagellar	throughout	diaulic	Alder & Hancock 1854b Alder & Hancock 1855 Bergh 1888, Eliot 1906, Schmekel 1970
21 × 31.1.31	unknown	unknown	unknown	unknown	unknown	Eliot 1909
20 × 5.1.5	unknown	unknown	unknown	unknown	unknown	Baba & Abe 1970
18 × 24.1.24	proximal, semi-serial within female gland mass	absent	thick	throughout	trialucic	Marcus 1958
23 × 37.1.37	unknown	unknown	short	unknown	unknown	Eliot 1907
20 × 28.1.28	unknown	unknown	unknown	unknown	unknown	Bouchet 1975
20 × 10-20.1.10-20 19 × 25.1.25	proximal	absent	elongate, flagellar	throughout	trialucic	Baba & Abe 1970 present study
20 × 42.1.42 18 × 41.1.41 17 × 26.1.26	elongate, proximal, semi-serial	distal, minute	elongate, flagellar	throughout	diaulic	Bergh 1907 Barnard 1927 present study
18 × 21.1.21 22 × 26.1.26 20 × 20.1.20 21 × 21.1.21	short, proximal, semi-serial	distal, minute	conical	short	diaulic	present study

As mentioned in the discussion of the synonymy of *Antiopella* with *Janolus* the elaboration of the masticatory border and shape of the jaw are interspecifically variable (Fig. 26). Previous workers (Pruvot-Fol 1954; Marcus 1958) have emphasized the distinctness of a smooth versus denticulate masticatory border. However, *Janolus toyamensis* (Fig. 26C) possesses three large tubercles on the masticatory border and *J. novozealandicus* was described as having indistinct denticles (Eliot 1907).

The radular teeth are variable within *Janolus* (Fig. 27) and some intraspecific variations exists. The rachidian teeth are denticulate in *J. fuscus* (MacFarland 1966; present study), *J. comis* (Marcus 1958), *J. mirabilis* (Baba & Abe 1970), and *J. mucloc* (Marcus 1958), striate in *J. longidentatus* (present study), and smooth in the remaining species. The rachidian tooth has a broad base in species with denticulations or striations and is linear in species with smooth teeth. In *J. fuscus* (MacFarland 1966; present study), *J. mirabilis* (Baba & Abe 1970), and *J. mucloc* (Marcus 1958) the inner 1 to 3 lateral teeth are denticulate while the outer teeth are entirely smooth. *J. cristatus* generally has smooth lateral teeth (Alder & Hancock 1855), but exceptionally (Bergh 1874) they are denticulate. The presence or absence of denticles varies with age in *J. comis* (Marcus 1958) and *J. hyalinus* (Eliot 1906). Bouchet (1975) noted that the lateral teeth of *J. praeclarus* increase in size until the eighteenth row and then begin to diminish. In *J. australis* the innermost are largest (Bergh 1884). In *J. cristatus* (present study) and *J. capensis* (present study) the teeth increase in length on either side of the radula until about one-third of the breadth, and subsequently diminish. In *J. capensis* the radular morphology of fifteen specimens of various sizes did not vary significantly. In *J. hyalinus* (Eliot 1906) and *J. novozealandicus* (Eliot 1907), and in at least ten specimens of *J. longidentatus* (present study) the largest lateral teeth are found at or adjacent to the outer edge of the radula. The relative length of the base to the cusp of the lateral teeth varies considerably between species and appears to be useful in the separation of species.

The central nervous system of *Janolus cristatus* was described (Alder & Hancock 1851) as containing distinct cerebral and pleural ganglia. Bergh noted that these ganglia are fused in *Janolus australis* (Bergh 1884) and *J. capensis* (Bergh 1907). The present study confirms this arrangement in *J. capensis*, while *J. longidentatus* possesses distinct ganglia as in *J. cristatus*.

The morphology of the reproductive system has been fully described in five species of *Janolus*. In *J. comis* and *J. mucloc* (Marcus 1958) the arrangement is triaulic with a short uterine duct connecting the vagina and female gland mass near the separation of the oviduct and vas deferens from the ampulla. In *J. cristatus* and *J. hyalinus* (Schmekel 1970) the vagina joins the female gland mass only at the female atrium, producing an androdiaulic configuration. The present study has shown that *J. toyamensis* (Fig. 28G) has a triaulic arrangement with a proximal receptaculum seminis but with no bursa copulatrix. *J. capensis* and *J. longidentatus* have a diaulic arrangement with a proximal

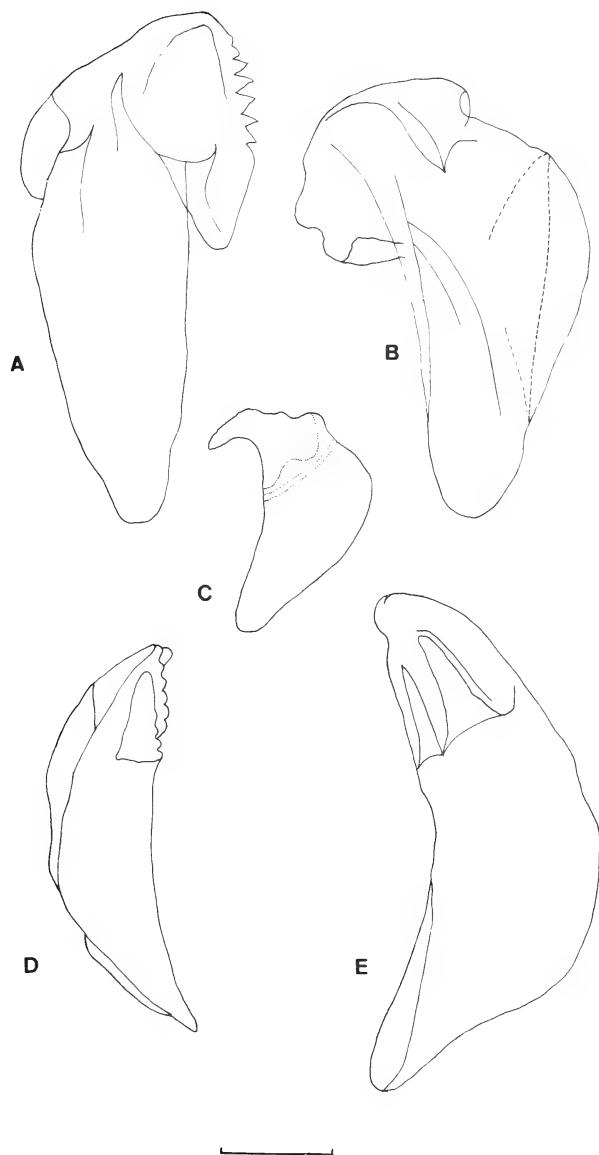


Fig. 26. Variation in jaw morphology. A. *Janolus fuscus* O'Donoghue, 1924. B. *Bonisa nakaza* gen. et sp. nov. C. *Janolus toyamensis* Baba & Abe, 1970. D. *Janolus longidentatus* sp. nov. E. *Janolus capensis* Bergh, 1907. Scale 1,0 mm.

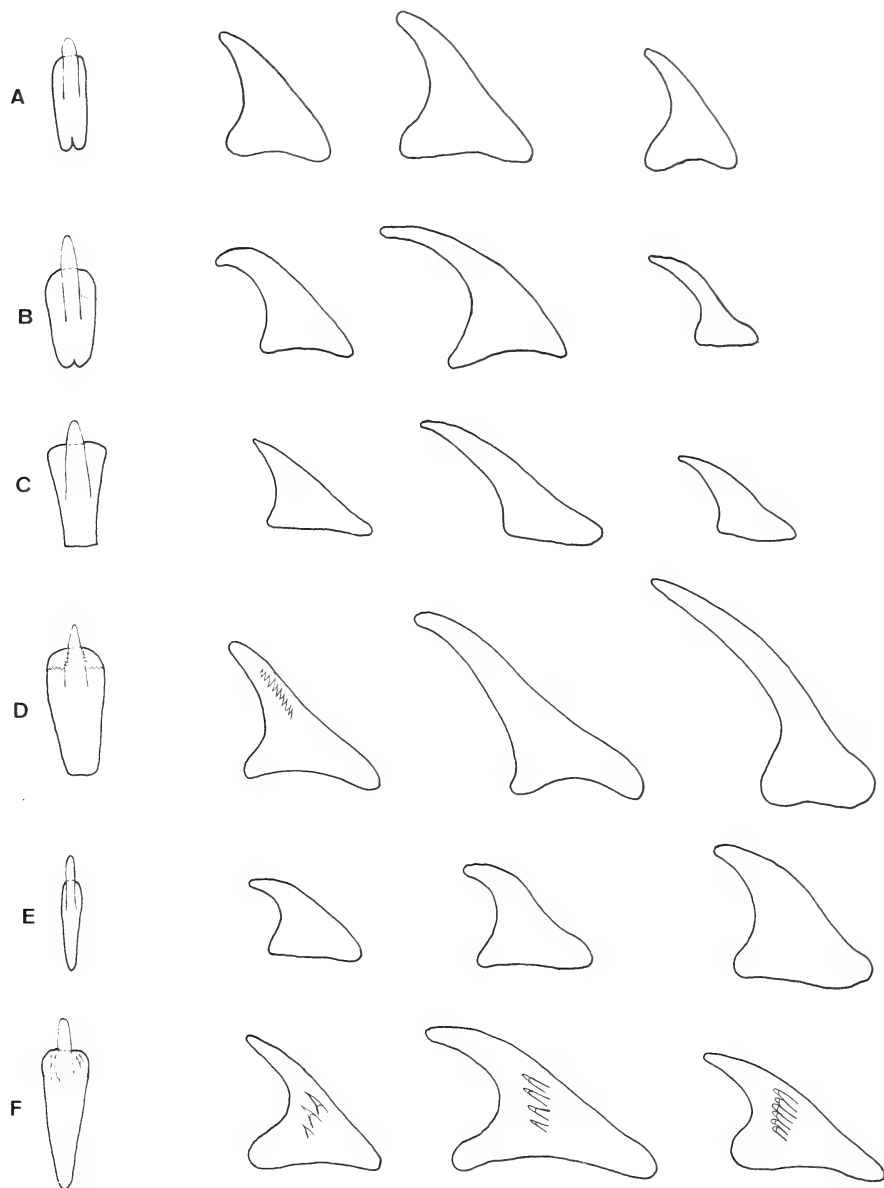


Fig. 27. Variation in the rachidian, first, seventh and twentieth lateral teeth in the Janolidae. A. *Janolus capensis* Bergh, 1907. B. *Janolus longidentatus* sp. nov. C. *Janolus cristatus* (Chiaje, 1841). D. *Janolus fuscus* O'Donoghue, 1924. E. *Janolus toyamensis* Baba & Abe, 1970. F. *Bonisa nakaza* gen. et sp. nov. Not drawn to scale.

receptaculum seminis and a minute, distal bursa copulatrix. This configuration is also present in *J. fuscus* (Fig. 28F) contrary to that described by MacFarland (1966, pl. 64 (fig. 11)).

The shape of the penis has been utilized as a characteristic for specific separation. *Janolus flagellatus* (Eliot 1906) was described as distinct from *J. hyalinus* because its elongate, flagellar penial papilla was thought to be different from the blunt papilla depicted by Bergh (1888) for *J. hyalinus*. Subsequent work by Schmekel (1970) has shown that the penis of *J. hyalinus* is flagellar when fully extended. The shape of the penis varies considerably within species depending on degree of extension. In comparing penial structure between species, it is imperative that descriptions be made from specimens with a fully extended penis.

The egg mass of *Janolus cristatus* (Alder & Hancock, 1855: pl. 44 (figs 6–7)) is a short, convoluted ribbon of about one and a half whorls, with a single egg per capsule. A similar egg mass is apparently present in *Janolus fuscus* (O'Donoghue 1924). The egg mass of *Janolus capensis* (present study) is globose, consisting of many whorls and with 38 to 45 eggs per capsule, while that of *J. longidentatus* is a flat spiral consisting of 5–9 eggs per capsule.

Janolus longidentatus differs from all other species of *Janolus* which possess denticles on the masticatory edge. *J. mucloc* (Marcus 1958) is triaulic and therefore differs from the diaulic *J. longidentatus*. *J. praeclarus* (Bouchet 1975), while much of its anatomy remains unknown, differs from *J. longidentatus* in its orange versus translucent white coloration, smaller inter-rhinophoral crest, branching of the ceratal ducts near the middle rather than basally, more sharply arched radular teeth that are longest near the middle rather than at the outer edge of the radula, and jaws with 6 denticles rather than 7 or 8. *Janolus longidentatus* differs from *J. fuscus* in its coloration, more elaborate inter-rhinophoral crest, smooth inner lateral teeth, and presence of anal glands. *Janolus longidentatus*, although similar to *J. cristatus* in coloration, external and reproductive anatomy (Schmekel 1970), differs in several significant aspects. In *J. longidentatus* the ceratal ducts branch basally while they branch apically in *J. cristatus*. The rachidian teeth of *J. longidentatus* are broad with striations versus the smoothly linear form of *J. cristatus*. In *J. cristatus* the radular teeth are largest at the inner third of the radula, while they are broadest near the outer margin in *J. longidentatus*. The lateral teeth are broader and heavier in *J. cristatus*. The oviduct is short in *J. cristatus* and elongate in *J. longidentatus*. *J. cristatus* has a blunt club-shaped penis, while in *J. longidentatus* it is conical.

Despite the difference in the elaboration of the masticatory border of the jaw, *J. longidentatus* most closely approaches *J. capensis* in its morphology. For this reason a morphological comparison of the three sympatric South African janolids is provided in Table 3.

The South African species of janolids occur together in the shallow waters of False Bay. All three species can be found within a few centimetres of each other. *Janolus capensis* and *J. longidentatus* have been observed to feed upon

TABLE 3
Comparative morphology of South African janolids.

	<i>Bonisa nakaza</i>	<i>Janolus capensis</i>	<i>Janolus longidentatus</i>
body	stout	stout	slender
inter-rhinophoral crest	low, few convolutions	high, many convolutions	high, many convolutions
ceratal ducts	absent	multifid, irregular, near middle	quadrifid, regular, near base
gonopore	near middle of body	near middle of body	anterior third of body
nephroproct	posterior third of body	posterior to middle of body	near middle of body
mouth opening	oblong	oblong	round
salivary glands	with basal reservoir	taper at insertion	glandular at insertion
masticatory border	smooth	smooth	7-8 denticles
rachidian tooth	broad, with large denticles	smooth, linear	broad, with striations
largest laterals	innermost teeth	third of width of radula	near outer margin of radula
lateral teeth	hook-shaped, denticulate	hook-shaped, smooth	with elongate cusp, smooth
cerebral and pleural ganglia	distinct	fused	distinct
penis	club-shaped, corrugated	flagellar	conical
vas deferens	short, straight	highly convoluted	with few convolutions
receptaculum seminis	large, saccate	elongate, as long as vagina	short, quarter of vaginal length
eggs/capsule	1 or 2	38-45	5-9

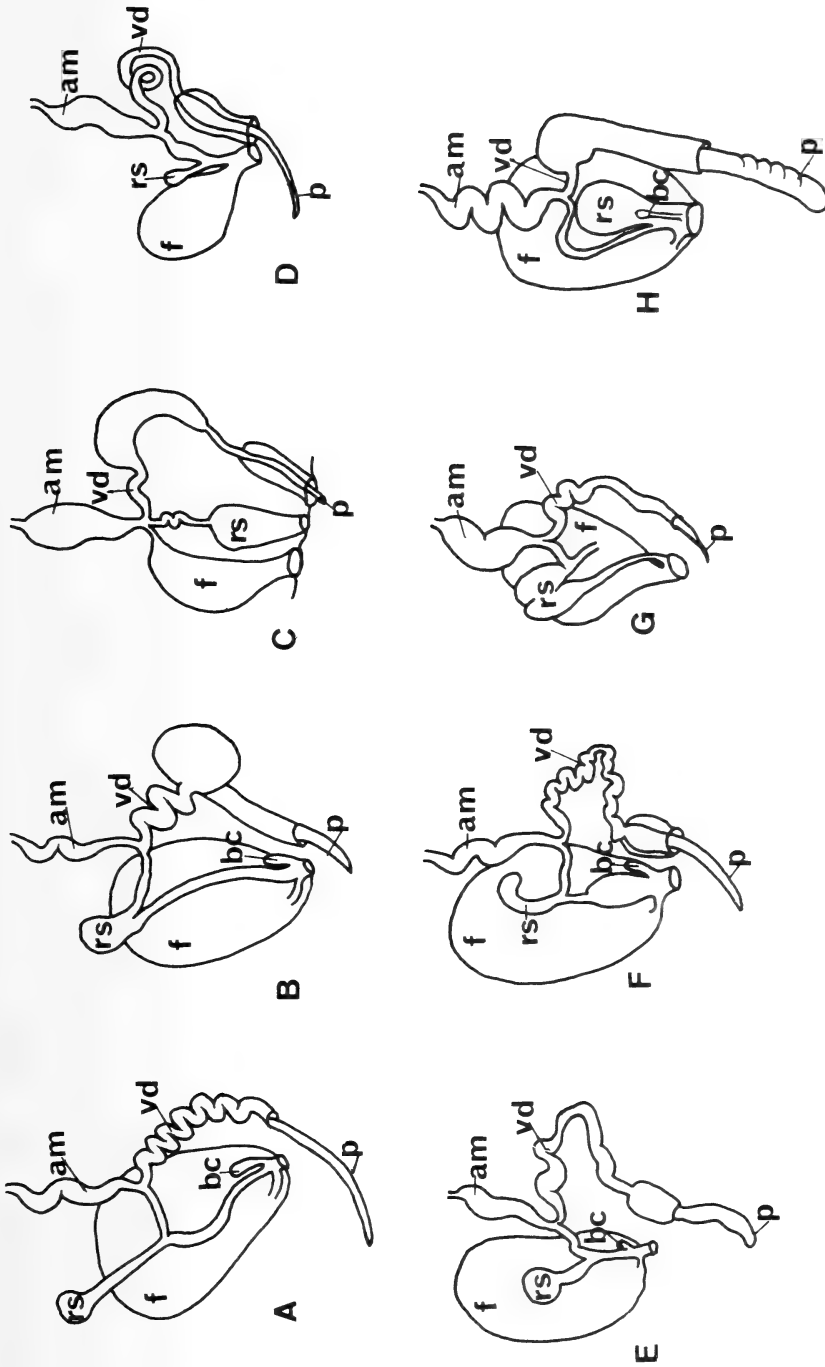


Fig. 28. Variation of reproductive system in *Janolus*. A. *Janolus capensis* Bergh, 1907 (present study). B. *Janolus longidentatus* sp. nov. (present study). C. *Janolus comis* Marcus, 1955 (after Schmckel 1970). D. *Janolus hyalinus* (Alder & Hancock, 1854) (after Schmckel 1970). E. *Janolus cristatus* (Chiaje, 1841) (after Schmckel 1970). F. *Janolus fuscus* O'Donoghue, 1924 (present study). G. *Janolus toyamensis* Baba & Abe, 1970 (present study). H. *Bonisa nakaza* gen. et sp. nov. (present study). Not drawn to scale.

the same species of ectoproct, while *Bonisa nakaza* feeds on a more heavily calcified species. Food abundance does not appear to be a limiting factor as many ectoproct colonies are devoid of janolids. Observation of feeding behaviour in *Janolus capensis* and *J. longidentatus* has produced no apparent differences in mode of feeding or handling of prey. No obvious form of resource partitioning has been observed between the two species, although it may exist.

The hottentot, *Pachymetopon blochii*, is the most common fish species in environments where janolids have been observed and is known to be a generalized omnivore of benthic organisms (Nepgen 1977). Specimens of *Bonisa nakaza*, *Janolus capensis*, and *J. longidentatus* are readily ingested by hottentots in the field and even more readily regurgitated in an unharmed state, suggesting defensive immunity to fish predation. More detailed study of the three species of janolids is required to determine their competitive population dynamics, interaction, and possible resource partitioning.

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ABBREVIATIONS

a	anus	i	intestine
ag	anal glands	m	muscle bands
al	albumen gland	me	membrane gland
am	ampulla	mu	mucous gland
b	buccal mass	n	nephroproct
bc	bursa copulatrix	o	oral glands
c	cerebral ganglion	p	penis
cp	cerebropleural ganglion	pg	pedal ganglion
d	digestive gland branch	pl	pleural ganglion
dg	digestive gland	rc	renopericardial canal
e	eye	rs	receptaculum seminis
f	female gland mass	s	stomach
g	gonopores	sg	salivary gland
ga	ceratal ganglion	vd	vas deferens
gl	ceratal gland		

6. **SYSTEMATIC** papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family *Nuculanidae*
Nuculana (Lembulus) bicuspidata (Gould, 1845)
Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

- (a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
- (b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- (c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

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Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

TERRENCE M. GOSLINER

THE SOUTH AFRICAN JANOLIDAE
(MOLLUSCA, NUDIBRANCHIA)
WITH THE DESCRIPTION OF A NEW GENUS
AND TWO NEW SPECIES

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OCTOBER 1981

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ANNALS

OF THE SOUTH AFRICAN
MUSEUM

CAPE TOWN



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Title: informative but concise, without abbreviations and not including the names of new genera or species
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- (d) *Introduction*
- (e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
- (f) *Summary*, if paper is lengthy
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- (h) *References*
- (i) *Abbreviations*, where these are numerous

3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

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Footnotes should be avoided unless they are short and essential.

Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

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FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch.*, Paris 88: 100-140.

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(continued inside back cover)

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DESCRIPTION OF
SOME JUVENILE HOMINID SPECIMENS
FROM SWARTKRANS, TRANSVAAL

By

F. E. GRINE

Cape Town Kaapstad

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By

F. E. GRINE

South African Museum, Cape Town

(With 15 figures)

[MS accepted 12 May 1981]

ABSTRACT

Recent work on the hominid fossils from Swartkrans revealed several juvenile specimens which required cleaning and description. Four such specimens, representing the gnathic and/or dental remains of three 'robust' australopithecine individuals, have been prepared and described in detail. The specimens, SK 839/852, SK 1595, and SK 2147 have added a number of deciduous and permanent teeth to the collection from this site.

CONTENTS

	PAGE
Introduction	43
Material and descriptions	45
Specimen SK 839	45
Deciduous dentition	45
Permanent dentition	50
Specimen SK 852	53
Deciduous dentition	54
Permanent dentition	58
Specimens SK 839/SK 852 composite	61
Specimen SK 1595	62
Deciduous dentition	63
Permanent dentition	65
Specimen SK 2147	67
Discussion	69
Acknowledgements	69
References	70

INTRODUCTION

Since 1948, when Robert Broom and J. T. Robinson began working at Swartkrans, the fossiliferous deposits of this cave system have yielded an abundance of hominid remains, including a number of juvenile specimens.

Geological and palaeontological investigations have demonstrated that the Swartkrans deposit consists of older and younger sediment groups (Brain 1958, 1976; Cooke 1963, 1978; Brain, Vrba & Robinson 1974; Hendey 1974; Vrba 1975; Butzer 1976). Butzer (1976) and Brain (1976) have defined the older breccias as Member 1 and the younger breccias as Member 2 of the Swartkrans Formation.

The first hominid specimens recovered from the Swartkrans Formation were attributed to a new taxon, *Paranthropus crassidens*, by Broom (1949). The vast majority of hominid specimens which have been found at Swartkrans (over 95 % of individuals) have been referred to this taxon under a variety of names, viz. *Paranthropus crassidens*, *P. robustus*, *Australopithecus crassidens*, *A. robustus*, and *A. robustus crassidens*. Geological studies have shown that these australopithecine remains are derived from the Member 1 sediments (Brain 1976, 1978).

The existence of individuals of the genus *Homo* in the Swartkrans deposit has been well substantiated (Broom & Robinson 1949, 1950, 1952; Robinson 1953*a*, 1953*b*, 1961; Tobias 1968, 1978; Clarke, Howell & Brain 1970; Clarke & Howell 1972; Wallace 1972, 1975; Clarke 1977*a*, 1977*b*; Olson 1978). The first specimen referable to *Homo* to be found at Swartkrans was the mandible SK 15 (Broom & Robinson 1949, 1950). The jaw was found in a pocket of brownish breccia surrounded by the typically pink Member 1 sediments, and it was initially thought that SK 15 was younger than the australopithecine remains (Broom & Robinson 1949, 1950). Later, however, Robinson (1953*b*) considered that the brown breccia encasing the mandible was a pocket of decalcified primary breccia and that SK 15 and the australopithecine remains were coeval. More recent work has demonstrated that the brown breccia is, indeed, younger than the australopithecine-bearing Member 1 sediments (Brain, Vrba & Robinson 1974; Brain 1976, 1978).

Three other hominid specimens, a P_3 (SK 18*a*), a proximal radius (SK 18*b*), and the buccal moiety of a P_4 (SK 43), were recovered from within the same pocket of Member 2 breccia as the SK 15 mandible. These four specimens have been referred to the same taxon (Broom & Robinson 1950, 1952; Robinson 1953*b*; Tobias & Wells 1967).

Several specimens attributed to *Homo* (e.g. SK 45, SK 847, SK 27, and SK 2635) have been recovered from the australopithecine-bearing Member 1 breccia. As noted by Clarke (1977*a*), there is little morphological basis for assuming that the *Homo* specimens from Members 1 and 2 belong to the same specific taxon. On the other hand, it is generally accepted that the australopithecine remains from Swartkrans are representative of a single, species-specific taxon (Broom & Robinson 1952; Robinson 1956; Tobias 1967; Wallace 1972; Clarke 1977*a*; Howell 1978).

Recent work on the hominid fossils from Swartkrans revealed several juvenile specimens which required cleaning, reconstruction and description. Four such fossils are dealt with in this paper. The specimens consist generally of small gnathic fragments with variously preserved deciduous and permanent teeth. The fossils are catalogued in the Transvaal Museum as SK 839, SK 852, SK 1595, and SK 2147, and all are derived from Member 1 breccias.

Each specimen will be described as follows: (i) the data presented on the relevant museum catalogue card, (ii) a brief statement of preservation prior to cleaning and reconstruction, and (iii) a detailed morphological description of the specimen after restoration.

All measurements recorded here were taken by the author, unless stated otherwise. The dental measurements were taken to 0,1 mm accuracy with a dial-equipped sliding vernier caliper.

MATERIAL AND DESCRIPTIONS

SPECIMEN SK 839

This specimen was excavated from Member 1 breccia by J. T. Robinson in 1952. The description on the catalogue card reads: 'Fragmentary juvenile maxilla containing some deciduous and permanent teeth some of which have suffered considerable damage.'

Prior to restoration, this specimen consisted of isolated, incompletely developed and slightly damaged LM¹ and RM¹, isolated and slightly damaged Rdm² and the distal two-thirds of the Rdm¹. In addition, the badly damaged permanent incisors, the damaged Rdi¹, the root of the Ldi¹, and a small bit of the alveolar portion of the maxilla were preserved in a piece of breccia (Fig. 1).

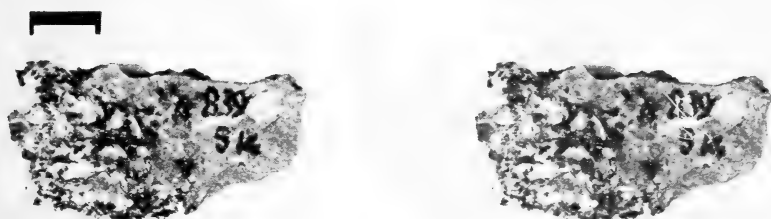


Fig. 1. Stereoview of the maxillary central deciduous and central and lateral permanent incisors of SK 839 prior to preparation. Compare with Figures 2-5. Scale in cm.

The crown of the Ldi¹ was found in a box with another, unrelated, hominid specimen from Swartkrans. The two deciduous central incisors and the four permanent incisors were cleaned, reconstructed and strengthened by the author.

Deciduous dentition (Figs 2-4)

Maxillary central deciduous incisors

The damaged crowns and roots of both incisors are present. The crown of the Ldi¹ is only moderately well preserved; the distolingual quadrant is missing and the remaining lingual portion is separated from the buccal part by a narrow crack. The buccal surface is displaced somewhat by virtue of breaks on either side of a 0,7 mm wide vertical sliver of enamel. The crown of the Rdi¹ is better preserved, with small pieces of both the mesial and distal edges missing. The roots of both teeth are poorly preserved; the lingual sides of both are missing just beyond the cervical lines, and the buccal surfaces are covered by remnants of the alveolar portion of the maxilla.

Occlusal wear is moderate in degree, with some reduction of crown height; most of the lingual aspect comprises a lingually sloping and slightly mesiodistally concave dentine exposure. The buccal edge of this surface is rather sharp and comprises a thin wall of enamel. Lingually, the remaining enamel surface shows slight faceting. Interproximal attrition is moderate on the mesial face, with dentine exposed on the incisal aspect of this surface; distally, interproximal wear appears to be slightly less severe. Neither crown shows any perikymata, but on the buccal surface of the Ldi¹ there is a rather large hypoplastic area (MD, 1,0 mm; height, 0,6 mm) surrounded by several smaller pits, whilst on the Rdi¹ a considerably smaller, single hypoplastic pit is evident.

The buccal aspect of the crown appears to have been square in outline before wear. There is no cervical enamel prominence, and this surface is nearly flat and disposed vertically incisocervically. Wear and damage to the incisolingual aspect of the crowns have obliterated any morphology that might have been present.

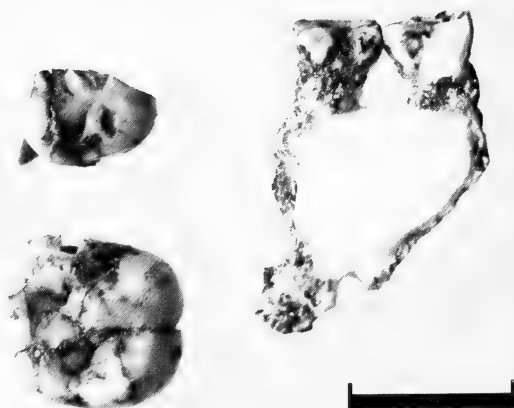


Fig. 2. Lingual view of the maxillary central deciduous incisors; and occlusal view of the Rdm¹ and Rdm² of SK 839.
Scale in cm.

Robinson (1956: 122) recorded the existing mesiodistal diameters of both crowns as 5,7 mm and noted that, because of the appreciable degree of incisal and interproximal wear, the original dimensions 'must have been about a millimetre greater'. The author agrees with Robinson that about 0,5 mm of dental material has been lost from either side of each crown. The dimensions of these teeth recorded by the present author are as follows:

	MD diameter (as measured)	MD diameter (estimated)	BL diameter (estimated)
Ldi ¹	5,7 mm	6,7 mm	5,2 mm
Rdi ¹	5,8 mm	6,8 mm	5,2 mm

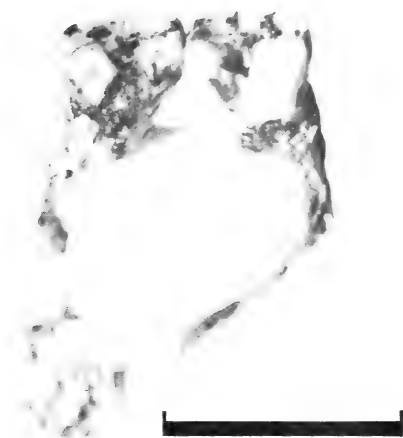


Fig. 3. Oblique incisolingual view of the maxillary deciduous central incisors of SK 839, showing type of wear. Scale in cm.



Fig. 4. Buccal view of maxillary central deciduous incisors and the attached alveolar bone of SK 839. Scale in cm.

Maxillary first deciduous molar

The distal two-thirds or more of the right crown is preserved. The portion of the crown that is missing has been broken away along a line which runs obliquely buccolingually from a point apparently just behind the tip of the paracone, through the protocone to the level of the lingual developmental groove. A slight crack runs distally from the paracone, through the tip of the metacone where it bifurcates, one limb courses distobuccally, whilst the other divides the distal marginal ridge. The mesiobuccal root is missing, and the lingual root has been broken away from the crown with the cervical enamel margin. The distobuccal root is preserved for what appears to be most of its length. It is evident that buccally the neck of the radicular system was rather low, there being less than 1 mm of cementum exposed between the cervical enamel margin and the point of bifurcation of the two buccal roots. The distobuccal root, as preserved, slopes away from the crown both distally and very slightly buccally. The root is straight and the apical end appears to taper slightly.

It is evident that all four principal cusps—paracone, metacone, protocone and hypocone—were present. The size of the paracone cannot be determined accurately, but it seems to have been approximately the same size as, or perhaps slightly smaller than, the metacone. The protocone was apparently the largest cusp. The hypocone and metacone are almost the same size. Occlusal wear is moderate and has produced two bevelled surfaces. Mesially, the protocone has been worn flat and a moderately large, concave dentine island is exposed. The protocone is worn slightly below the level of the paracone, which appears to have shown a very small dentine exposure. The distal portion of the occlusal surface slopes distolingually; a moderate-sized, concave dentine island is exposed on the hypocone, while no dentine is shown on the metacone. Interproximal attrition appears to have been slight to perhaps moderate in degree. The distal contact facet, which measures approximately 3,1 mm buccolingually by 2,1 mm in height, is ovoid in outline and flattened. It is located, for the most part, behind the hypocone, while the corresponding facet on the dm² is situated over the buccal half of its mesial face.

The buccal face, as preserved, shows no cervical prominence or swelling, and it is faintly convex occlusocervically. There is no trace of a buccal groove. The cervical margin of the lingual face is not preserved, but this surface—over the hypocone—is more convex than the buccal surface. The lingual groove is very shallow and short.

The protocone and paracone appear to have been separated by a very shallow, narrow groove. The trigon basin is represented by a short and narrow but oblique groove. The distal trigon crest is narrow but continuous. The distal marginal ridge is thick and high, extending without any apparent interruption from behind the tip of the metacone to the hypocone. The talon basin, or fovea posterior, is represented by a crescent-shaped, relatively deep groove.

It is not possible to record any crown diameters for this tooth.

Maxillary second deciduous molar

The crown of the right tooth is preserved. It is very nearly complete; the cervical margin has been damaged round the entire periphery save for the buccal aspect. A large, vertical sliver of enamel has broken away from the mesial face, and the distobuccal corner of the crown has been displaced slightly. Several narrow cracks traverse the crown. The radicular system has been broken away save for a short segment of the mesiobuccal root.

Viewed from the occlusal aspect, the crown is square in outline. All four principal cusps are present and well developed. The protocone is by far the largest cusp, followed by the metacone and the paracone, the latter being slightly smaller. The hypocone is well developed and is approximately the same size as the metacone. Occlusal wear is slight, and has reduced the cuspal tips to nearly the same height. Wear is heaviest on the protocone, which shows large enamel facets but only a tiny pit of exposed dentine. Small dentine exposures are displayed also by the metacone and paracone. Generally, the mesial portion of the crown has been worn more heavily than the distal part. Interproximal contact with the dm^1 appears to have been slight, while no distal contact facet is present.

The mesial marginal ridge is thick and well developed and, though worn, it appears to have coursed without interruption from the front of the paracone to the protocone. Distal to the mesial marginal ridge, the fovea anterior is represented by a short, narrow groove which is completely enclosed distally by a short and thin but continuous epicrista. The epicrista runs parallel to the mesial marginal ridge. The trigon basin is broad and rather deep, its floor being represented by a triradiate groove. The distal trigon crest is moderately well developed but is incised and thinned in its middle by a narrow but deep groove. The distal marginal ridge is moderately thick and high and runs without interruption from the metacone to the hypocone. It is slightly lower in its middle, with two faint grooves on its mesial aspect; it runs continuously, high up on to the metacone. The talon basin is represented by a deep, broad groove which runs obliquely between the hypocone and protocone to incise the lingual surface of the crown.

The buccal surface is rather flat and vertically disposed over the upper third of its height, and is slightly swollen and convex over the cervical two-thirds. There is no distinct cervical enamel prominence, and the cervical enamel line courses, for a short distance, towards the bifurcation of the two buccal roots. The buccal groove is rather weakly expressed; it is broad but very shallow towards its occlusal end, and courses cervically for less than half of the height of the crown where it terminates gradually. A number of very small hypoplastic pits cover the buccal face around both the occlusal and cervical extremities of the buccal groove.

The lingual surface is more convex than the buccal, and curves in a continuous arc from the occlusal margin to the cervical line. The cervical enamel margin is missing, but it appears that no pronounced prominence was

present. The lingual groove is deep and broad over most of its course, but terminates gradually approximately half-way towards the cervical margin. There is no trace of a Carabelli trait. The protocone is ringed on its mesial and lingual aspects by a thin band of numerous, tiny, hypoplastic pits. This band is situated near the occlusal surface.

The radicular system is represented solely by a short segment of the mesiobuccal root. In so far as it is preserved, it courses slightly mesialward and is considerably broader in its buccolingual than in its mesiodistal dimension. It appears that the radicular neck was low.

Robinson (1956: 128) recorded the mesiodistal and buccolingual diameters of this crown as 10,5 mm and 11,4 mm respectively. The measurements obtained by the present author are as follows:

	MD diameter (as measured)	MD diameter (estimated)	BL diameter (as measured)
Rdm ²	10,7 mm	10,8 mm	11,5 mm

Permanent dentition (Fig. 5)

Maxillary central permanent incisors

The left and right maxillary central incisors are represented. Both teeth consist of rather badly damaged crowns only. They are unerupted. A root is not present.

The crowns were badly crushed and broken in preservation, and both have been reconstructed from several different pieces. The left crown is crushed and the central and distal regions of the lingual surface have been displaced. The mesial, buccal and distal surfaces have suffered considerable loss of enamel about the cervical margin. The mesiobuccal quadrant of the left crown is missing, and the mesial end of the lingual surface has suffered slight crushing.

The mesial end of the incisal edge is slightly rounded, while the distal extremity of this edge shows a broad curvature. The incisal edge comprises large mesial and distal mammelons and a considerably smaller and lower median mammelon. Viewed from the buccal aspect, the crown is judged to have had a tapered outline, the cervical region having been narrower than the incisal portion. The buccal surface is gently convex incisocervically. Neither tooth exhibits either perikymatous or hypoplastic enamel.

Lingually, there is a moderate cervical enamel swelling which appears to have been symmetrically disposed. The mesial marginal ridge is much more pronounced, and a relatively narrow, low median ridge projects vertically from the cervical enamel prominence towards the incisal edge. The lingual surface is slightly concave over the upper half of the crown, both incisocervically and mesiodistally.

	MD diameter (as measured)	MD diameter (corrected)	BL diameter (corrected)
LI ¹	8,2 mm	8,6 mm	—
RI ¹	8,6 mm	8,6 mm	6,8 mm

Maxillary lateral permanent incisors

The crown of the right tooth is well preserved, with only slight damage to parts of the cervical enamel margin. The crown of the left tooth is severely crushed and distorted and, because the right crown is so well preserved, it was deemed unnecessary to attempt a reconstruction of its antimeres.

The tooth is unerupted. There is no root present. The crown appears to be completely developed.

The mesial end of the incisal edge is gently rounded, while the distal extremity is slightly lower than the mesial and is more broadly rounded. The incisal edge is gently rounded and rather smooth; there is no mammelon development.

Viewed from the buccal aspect, the crown has a tapered outline, with the cervical region narrower than the incisal portion. The buccal surface is slightly convex incisocervically, with a faint, broad, flattening in the centre of this surface over the upper half. This area is bounded both mesially and distally by faint ridges that course from the cervical region to the respective corners of the incisal edge. The distal side of this face displays several faint perikymatous ridges; there is no evidence of hypoplastic enamel.

Lingually, the cervical region shows a slight swelling. The mesial marginal ridge is slightly developed, the distal marginal ridge is moderately well developed and there is no median ridge present. The mesial and distal marginal ridges converge cervically to blend into the cervical swelling. The lingual surface is slightly concave, especially mesiodistally.

	MD diameter (as measured)	BL diameter (as measured)	Height (as measured)
RI ²	6,0 mm	5,5 mm	8,7 mm

Maxillary first permanent molars

The unerupted crowns of both the left and right maxillary first permanent molars are present. Both crowns have suffered from damage to the cervical enamel; generally, the right tooth is better preserved. The buccal side of the left crown is separated and displaced from the rest of the tooth by a crack which runs through the tips of the paracone and metacone. Nothing of the radicular system is present.

The two crowns are nearly identical in morphological detail (Fig. 5). Viewed from the occlusal aspect, the crown is nearly square in outline, with all four principal cusps present and well developed. The protocone is the largest cusp, followed by the paracone and metacone, which are nearly equal in size. The hypocone is the smallest cusp. The mesial marginal ridge is moderately thick; it is higher and thicker near the protocone where a moderate-sized protoconule is present. The protoconule is delineated on either side by shallow grooves. A short epicrista projects from the mesial end of the paracone and, although this crest is delineated on either side by deep, narrow grooves, there is

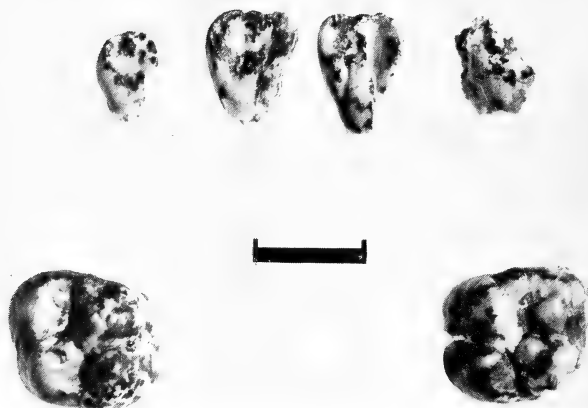


Fig. 5. Lingual view of the permanent incisors and occlusal view of the first permanent molars of SK 839. Scale in cm.

no anterior fovea present. The trigon basin is deep. The distal trigon crest is moderately thick, but is incised midway between the protocone and metacone by a relatively deep pit which is continuous with the deep, but narrow, groove between the protocone and hypocone. On the lingual surface this groove continues vertically for approximately half of the crown height, where it ends abruptly.

The lingual surface projects from the occlusal to the cervical margin; the cervical half of this face is slightly convex. The mesiolingual corner of the protocone presents two short, vertical grooves which are separated by approximately 2,7 mm of enamel. However, there is no alteration of the general curvature of this face. The Carabelli feature is represented by grooves. This feature is only slightly expressed on the left crown.

The buccal surface is less expanded than the lingual and is only faintly convex occlusocervically. The buccal groove is vertically deep and narrow and extends only over the upper third of the crown. It ends abruptly. Neither the buccal nor the lingual surface shows any indication of hypoplastic enamel.

Robinson (1956: 81) considered these crowns to be incompletely developed and recorded estimated, complete mesiodistal and buccolingual dimensions of 13,2 mm and 13,9 mm respectively. The present author agrees with Robinson that the crowns are immature, but he is unable to judge accurately how much, if any, additional increase in size would have been attained. The measurements of the crowns as recorded are as follows:

	MD diameter (as measured)	BL diameter (as measured)
LM ¹	12,5 mm	—
RM ¹	12,8 mm	14,0 mm

SPECIMEN SK 852

This specimen was excavated from Member 1 breccia by J. T. Robinson in 1952. The description on the catalogue card reads: 'Poor specimen of juvenile mandible with left dm_1 (broken); dm_2 , moderately worn; right dm_1 appreciably worn; dm_2 moderately worn and incomplete; and fragment of M_1 erupting.'

Prior to cleaning and restoration, this specimen consisted of an isolated and nearly complete Rd_c as well as the isolated, complete crowns of the LI_1 , LI_2 and $L\bar{C}$. The major part of this specimen consisted of the poorly preserved mandibular corpora with the roots of the Ldm_1 , the damaged Rdm_1 , Ldm_2 , Rdm_2 and the metaconid of the RM_1 , and the matrix-covered crown of the LM_1 (Fig. 6). The mandibular corpora were preserved in misalignment, and wedged

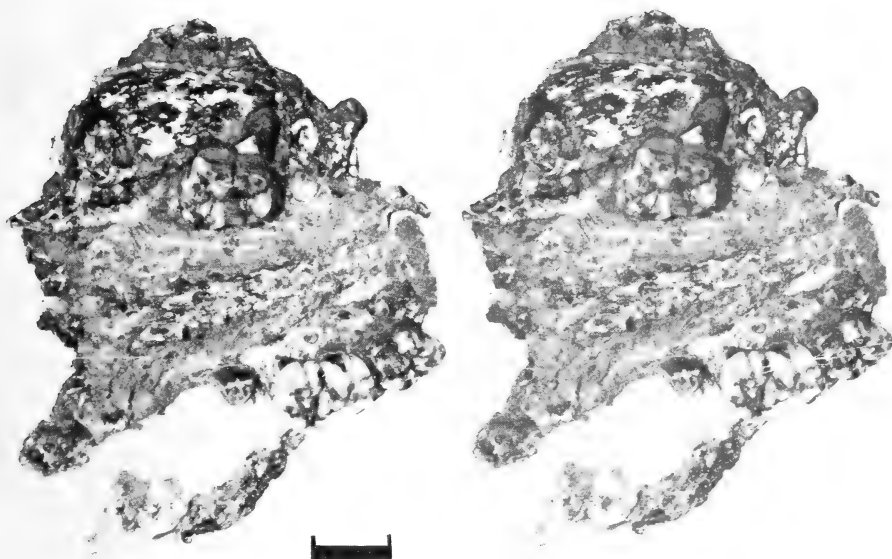


Fig. 6. Stereoview of the mandibular corpora and dentition of SK 852 prior to restoration. Compare with Figure 8. Scale in cm.

between them was a large piece of unidentified bone. The region of the RM_1 was covered in plaster. The two corpora were removed from the matrix and cleaned. In this process the hypoconid and hypoconulid of the RM_1 were discovered beneath the plaster; this piece of crown was reconstructed in correct anatomical position. The corpora and their contained teeth were cleaned and, where necessary, strengthened with plaster.

The mandibular corpora are poorly preserved, somewhat distorted and very incomplete. Meaningful descriptions or measurements for either of these are not possible (see Figs 8 and 10).

*Deciduous dentition (Figs 7-9)**Mandibular deciduous canine*

The right tooth only is present. It is reasonably well preserved with rather severe damage to the mesial portion of the crown, but the root is nearly complete with only the apical tip missing.

Enamel from the mesial and mesiolingual parts of the crown has been broken away. The tip is damaged also and a moderately wide vertical crack courses across the middle of the buccal surface.

Viewed from the buccal aspect, the crown is rather 'mitten-shaped' with a large primary cusp situated mesially and a small distal cuspid. The buccal surface is faintly convex incisocervically over the cervical third of the crown's height, and a cervical prominence is not present. The distal cuspid is worn, but there remains the trace of a short, faint vertical groove between it and the main cusp.



Fig. 7. Stereoview of the lingual aspect of the Rd_c of SK 852.
Scale in cm.

Lingually, there is a slight cervical prominence which is skewed distally. There are no tubercles supported by this prominence. The cervical enamel line courses downwards from mesial to distal. The mesial third of this surface has been damaged. A moderately deep, triangular-shaped groove separates the main cusp from the distal cuspid. A moderate enamel ridge courses from the tip of the distal cuspid downwards to blend into the cervical enamel prominence.

Occlusal wear is slight. A well-developed enamel facet is present along the distal slope of the main cusp and on the tip of the distal cuspid. This facet is narrow but highly polished, and it is continuous along the main cusp to a horizontal disposition on the distal cuspid. Dentine is not exposed. Interproximal attrition with the dm₁ was mild, with only a small, slightly flattened,

circular contact facet (0,7 mm diameter) near the top of the distal cuspid. The dimensions of the crown are as follows:

	MD diameter (as measured)	MD diameter (corrected)	BL diameter (as measured)	Height (estimated)
Rd _c	5,7 mm	5,9 mm	4,6 mm	6,5 mm

The root of this tooth is single. It has a flattened ovoid outline in cross-section, with the longer axis (5,1 mm) running from mesiobuccal to distolingual and the shorter axis (3,8 mm) running from mesiolingual to distobuccal. The root is rather straight and long. It is estimated that the original length was approximately 13,0 mm (measured length, 11,4 mm).

Mandibular first deciduous molars

The obliquely shorn-off roots of the left tooth and the somewhat damaged crown and roots of the right tooth are present. The right crown has suffered enamel loss along the entire distal surface, and the occlusal surface has a wide crack over the top of the hypoconid and metaconid. Two narrow, vertical cracks course across the buccal surfaces of the protoconid and hypoconid.

Viewed from the occlusal aspect, the crown has a somewhat irregular rectangular outline. The mesial end is slightly narrowed and projects anteriorly, while the distal end of the crown is broad and appears to have been flattened. The protoconid, hypoconid, metaconid, and entoconid are preserved. It appears that the hypoconulid was absent, or if it was present originally it is evident that it would have been very small. Wear and damage do not permit an accurate assessment of the relative cuspal sizes.

Occlusal wear is moderate, with considerable reduction and flattening of cuspal height. The occlusal surface has been worn so that a broad, rather flattened plane has been produced; this plane slopes slightly downward distally from the tips of the metaconid and protoconid. It appears that a small island of dentine was exposed on the top of the protoconid, while the metaconid shows a somewhat larger exposure. The top of the hypoconid is damaged, but it is evident that at least a moderately large dentine island was present. The entoconid is covered by a large, concave dentine basin. A second facet is present in front of the protoconid tip. This facet slopes downward mesially as a well-defined, polished enamel surface along the mesial marginal ridge.

Interproximal wear is judged to have been mild both mesially, as discussed above, and distally. Although the distal surface of the dm₁ is missing, the mesial surface of the dm₂ presents a moderate-sized, rectangular and somewhat flattened contact facet. On the Ldm₂ this facet measures 3,5 mm in breadth and 2,3 mm in height.

The mesial marginal ridge is relatively thick and courses round from in front of the protoconid to the mesial end of the metaconid. It is thicker buccally than lingually, where, mesial to the metaconid, it is considerably thinner. Nevertheless, the mesial marginal ridge is continuous around the front of the

tooth; it is not incised. Though the region is worn, it appears that a small plesioconulid might have been present mesial of the tip of the protoconid. The fovea anterior is represented by a short, relatively deep, transverse groove which is enclosed completely by the mesial marginal ridge and a continuous, high and moderately thick crest between the metaconid and protoconid. A broad contact is present between the metaconid and hypoconid, and the buccal groove is more mesial than the lingual groove.

The lingual surface is slightly convex occlusocervically with a faint cervical enamel prominence present. The lingual groove is faint and fades imperceptibly approximately half-way down this face.

The buccal surface over the hypoconid is rather bulbous in appearance and is moderately to markedly convex occlusocervically. A slight cervical enamel prominence is present. This face of the protoconid is convex over the cervical half, the occlusal half is somewhat flattened and slopes outwards cervically from the protoconid tip. A faintly developed tuberculum molare is present; the cervical portion of the protoconid surface projects slightly laterally and the cervical enamel line dips below the level of this margin on the hypoconid. The buccal groove is rather narrow, but relatively deep. It courses vertically to end abruptly about half-way down this surface.

A small area of hypoplastic enamel is present on the buccal surface of the protoconid, just mesial to the buccal groove.

The principal dimensions of the crown are as follows:

	MD diameter (as measured)	MD diameter (corrected)	BL trigonid (as measured)	BL talonid (as measured)
Rdm ₁	9,4 mm	10,0 mm	7,5 mm	8,1 mm

The radicular system comprises broad mesial and distal root plates and a very low neck. The two plates are directed almost vertically downward, expanding buccolingually towards their apical ends, and each has two separate radicular canals. The apical third of each root plate is bifid.

The apical ends of the mesial and distal radiculæ of the left tooth are separated on the buccal side by some 7,3 mm. The mesial root plate of the left tooth measures approximately 6,5 mm buccolingually at the cervical margin and 9,2 mm at the apical end. The distance from the cervical line to the buccal apex of the mesial plate is about 8,8 mm, and the lingual side of the plate measures some 9,3 mm in length.

Mandibular second deciduous molars

The left and right teeth are present. The left crown and root system are more complete than those of the right. The cervical half of the buccal surface and the upper part of the root of the left tooth are broken away.

On the right tooth most of the protoconid and hypoconid have been broken away, together with much of the distal root plate. Both crowns show several fine cracks which course across the surfaces in various directions; the

right tooth has been affected by this cracking more than the left. In so far as they are preserved, the crowns are nearly identical in morphological detail.

Viewed from the occlusal aspect, the crown is rectangular in outline. The five principal cusps are present and well developed. The metaconid is by far the largest cusp with the hypoconid, protoconid and entoconid nearly equal in size. The hypoconulid is, by a slim margin, the smallest cusp. In general, the cusps are rather bulbous in appearance, with narrow and nearly vertically sided grooves separating them.

Occlusal wear is slight, with all cusps showing enamel wear, though this is slightest on the entoconid. The other cusps have been reduced in height somewhat and they show flattened occlusal surfaces. The buccal cusps have been worn slightly more heavily than the lingual cusps. The tops of the protoconid, hypoconid, and hypoconulid are worn to a nearly flat, horizontal plane. Except for a small pit of dentine on the protoconid, there is no dentine exposure despite the reduction in cuspal height. Interproximal attrition with the dm_1 , as noted above, is slight, and there is no contact distally with the M_1 .

The mesial marginal ridge of the dm_2 is very thick and, though worn, it appears to have been relatively high. It continues uninterrupted from in front of the metaconid across to the protoconid. Behind this ridge the fovea anterior is represented by an H-shaped groove. The mesial transverse groove is narrow and relatively shallow, and it is incompletely enclosed behind by short, accessory transverse crests from the metaconid and protoconid. A short, narrow longitudinal groove separates these two crests. The distal transverse groove is somewhat longer, broader and deeper than the mesial groove, and it is completely enclosed behind by a very thick, continuous ridge between the back of the protoconid and the principal crest of the metaconid. The metaconid displays a broad contact with the hypoconid; the two buccal grooves, which surround the hypoconid, and the lingual groove, between the metaconid and entoconid, are arranged in a symmetrical Y-shaped pattern. The mesiobuccal developmental groove is thus situated mesiad of the level of the lingual groove. The distal marginal ridge is relatively thick and is uninterrupted in its course. This ridge is slightly worn but it is apparent that it supported a tiny accessory cuspid (the tuberculum sextum) which is represented solely by a faint convexity of the distal crown surface. The cuspid, despite its small size on the left tooth, is even smaller and more weakly expressed on the right crown. The fovea posterior is represented by a relatively deep but narrow crescent-shaped groove which is continuous with the talonid basin via a deep, narrow groove between the hypoconulid and entoconid.

The buccal surface has suffered damage. However, it is evident that the mesiobuccal groove was better developed than the distobuccal groove. The distal groove is relatively deep but narrow, and extends vertically for about one-third of the crown height where it terminates rather abruptly.

The lingual surface is somewhat inflated in appearance. It is slightly convex occlusocervically with a slight cervical enamel prominence at the base of the

metaconid and a rather marked prominence at the base of the entoconid. The enamel line continues round underneath the crown for a short distance between the mesial and distal radiculæ. The lingual groove is of moderate depth but narrow, and continues vertically to the cervical margin. Over the lower third of its course it is bifid, with a faint accessory groove running parallel to it mesially. The distal half of the metaconid surface displays a number of minute hypoplastic pits, and these are more numerous and marked near the lingual groove.

	MD diameter (as measured)	BL trigonid (as measured)	BL talonid (as measured)
Ldm ₂	12,2 mm	9,7+ mm	9,8+ mm
Rdm ₂	12,4 mm	—	—

The buccolingual diameters recorded here are minimum values; because of the damage the buccal surface has suffered, it is not possible to estimate accurately the original dimensions of the trigonid and talonid portions of the crown.

The root system of the second deciduous molar comprises broad mesial and distal radicular plates and a very low neck. Because of damage to the cervical region, the breadth of the plates cannot be measured accurately. The plates appear to diverge slightly as they course downward. The length of the buccal side of the mesial plate of the left tooth measures at least 10,5 mm.

Permanent dentition (Figs 8–9)

Mandibular central permanent incisor

The isolated crown of the left central incisor is present. The crown is complete and well preserved. A very short segment of the developing root is represented on the mesial and distal aspects of the tooth. The tooth had not yet erupted at the time of death.

The mesial and distal corners of the incisal edge are slightly rounded. A large, high mammelon is supported at either extremity, with a much lower tubercle between the mesial and distal mammelons.

Viewed from the buccal aspect, the crown has a high, tapered outline; the mesiodistal diameter is considerably greater incisally than cervically. The buccal surface is slightly convex incisocervically and a cervical enamel prominence is not present. Numerous faint, horizontal, perikymatous lines cover this face entirely.

Lingually, a moderate basal prominence is present. A tubercular structure is not supported by this swollen base. The basal prominence is symmetrically orientated. The mesial marginal ridge is thin and very faintly expressed; the distal marginal ridge is slightly better developed. The lingual surface is flattened.

	MD diameter (as measured)	BL diameter (as measured)	Height (as measured)
LI ₁	5,1 mm	5,7 mm	10,0 mm

Mandibular lateral permanent incisor

The isolated crown of the left tooth is present. The crown is well preserved and nearly complete, with only slight enamel loss to the buccal cervical margin and somewhat more severe damage to the base of the lingual side. The developing root is represented by short segments on the mesial and distal aspects of the tooth. The tooth had not yet erupted at the time of death.

The crown is somewhat more robust in appearance than that of the central incisor. The mesial and distal corners of the incisal edge appear rather sharply angulated with the mammelons at these extremities. The incisal edge is, in general, horizontal, and it supports five small mammelons.

Viewed from the buccal aspect, the crown is somewhat rectangular in outline. The mesiodistal breadth across the incisal portion is greater than that

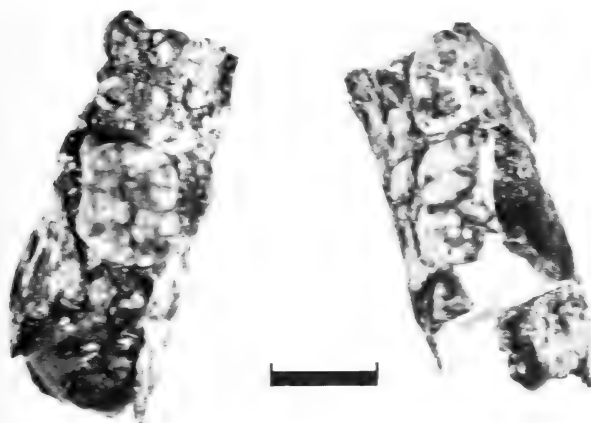


Fig. 8. Oculusal view of the mandibular corpora and dentition of SK 852 in approximate anatomical alignment. Scale in cm.



Fig. 9. Lingual view of the LČ, LI₂, LI₁, and Rd₂ (from left to right) of SK 852. Scale in cm.

across the cervical region of the crown, but the relative difference between these measurements is not so marked as in the central incisor. The buccal surface is slightly convex incisocervically. Very faint perikymatous lines and a broad but shallow groove are present on this face.

Although the cervical extremity of the lingual surface has been damaged, it is evident that a slight to moderate basal prominence was present. The basal swelling does not show tubercles. The mesial marginal ridge is slightly developed; the distal marginal ridge is more faintly expressed than the mesial. Between these ridges, the lingual surface is faintly concave both mesiodistally and incisocervically.

	MD diameter (as measured)	BL diameter (corrected)	Height (as measured)
LI ₂	5.6 mm	6.4 mm	9.9 mm

Mandibular permanent canine

The isolated crown of the left mandibular canine is well preserved and is nearly complete. The lingual cervical enamel margin has suffered only slightly from damage. Mesially, a short, thin sheet of the developing root is present, but this is not represented on any other part of the tooth. The tooth had not yet erupted at the time of death.

Viewed from the buccal aspect, the crown is nearly square in appearance; the mesial corner of the tip is slightly rounded, while the distal portion slopes downward for about half of the crown's height from just behind the centre of the crown. The tip of the tooth is obtuse; mesially this surface is nearly horizontal. The buccal surface is slightly convex occlusocervically as well as mesiodistally. No evidence of enamel pathology is shown on this face.

Lingually, the cervical prominence is moderate and symmetrical. Lingual tubercles are not present. The mesial marginal ridge is faintly expressed; it appears as a low, thin band coursing round from the occlusal surface of the crown for approximately half of the crown height, where it blends imperceptibly with the basal swelling. The distal marginal ridge is moderate; it originates occlusally approximately in the middle of the distal slope of the crown. This ridge becomes thickened towards the cervical prominence. A thin, low, vertical enamel ridge is situated mesiad of the distal marginal ridge, and this vertical crest originates at the cervical edge and continues cervically for just less than half of the crown height. The 'median' and distal marginal ridges are separated by a depression which is broader and relatively shallow occlusally, but which becomes increasingly narrower and deeper as it passes cervically, where it partially separates the distal ridge from the cervical swelling. The lingual surface is, for the most part, rather flat.

	MD diameter (as measured)	BL diameter (as measured)	Height (as measured)
LC.....	7.3 mm	8.1 mm	9.0 mm

Mandibular first permanent molar

The left crown is well preserved and complete. It is situated in its crypt and, except for the occlusal surface, only the distal surface and the posterior half of the buccal face are exposed. A narrow crack courses across the top of the hypoconulid and continues vertically over the distal surface. Slight enamel displacement has occurred along this crack. The root is represented by a relatively short sheet below the cervical margin, and it is evident that the mesial and distal root plates had begun development at the time of death. The right tooth is represented by a portion of the metaconid and a second piece of the crown containing parts of the hypoconid and hypoconulid. The remainder of the right crown is missing.

Viewed from the occlusal aspect, the crown appears to have a rectangular outline. All five principal cusps are present and are well developed. The metaconid seems to be the largest cusp, followed in decreasing order of size by the protoconid, entoconid, hypoconid, and hypoconulid.

The mesial marginal ridge has been damaged slightly but it appears to have been moderately well developed, thick and continuous. Distal to it, the fovea anterior is represented by a relatively short, but deep, transverse groove. The fovea is drained distally by a very narrow, but deep, groove between the protoconid and metaconid. An 'accessory' anterior fovea, as presented by the dm_2 , is not shown by this tooth. The principal crest of the metaconid has a short, distally deflected ridge (a deflecting wrinkle) which contains the hypoconid. The metaconid is more distally elongate than the protoconid. The lingual developmental groove is situated distad to the mesobuccal groove—and thus the primary occlusal fissure pattern is symmetrically Y-shaped. The distal marginal ridge is represented by a small cuspoid, the tuberculum sextum, which is demarcated from the hypoconulid and entoconid by shallow, narrow grooves. The fovea posterior is in the form of a small but relatively deep pit. A narrow groove between the entoconid and hypoconulid connects the fovea posterior with the distobuccal groove.

The posterior part of the buccal surface is slightly convex occlusocervically, and the distobuccal groove is deep but short. It courses vertically for slightly more than a third of the crown height, where it ends in a pit.

The dimensions of this crown cannot be determined accurately.

SPECIMENS SK 839/SK 852 COMPOSITE

The right first and second maxillary deciduous molars of SK 839 and the right first and second deciduous mandibular molars of SK 852 provide a contact between these two specimens. The occlusal relationships between both the first and second deciduous molars are very good (Fig. 109), and they are very similar in their general state of wear. Casts were made of the upper and lower second deciduous molars with the materials and according to the techniques described by Grine (1977). The occlusal surfaces of the casts were examined by scanning

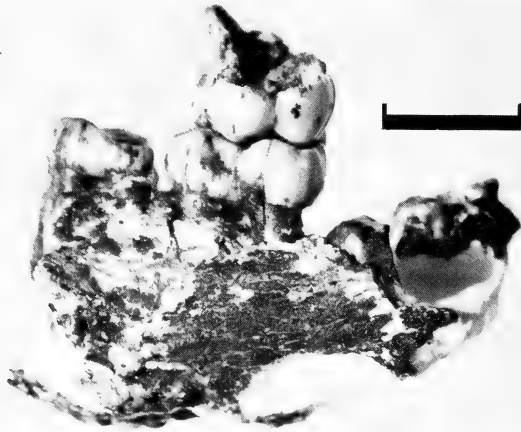


Fig. 10. Lingual view of the occlusal relationship between the Rdm^2 of SK 839 and the Rdm_2 of SK 852. Scale in cm.

electron microscopy. The types, degree, and orientation of the abrasive scratches on the two teeth were found to be very similar.

Also, the permanent teeth of the two specimens display degrees of calcification that are compatible with their having belonged to the same individual. The states of preservation of these fossils, for example the manganese staining patterns of the teeth, are also similar.

These findings support Wallace's (1972, 1973, 1978) suggestion that SK 839 and SK 852 represent the maxillary and mandibular remains of a single juvenile individual.

SPECIMEN SK 1595

This specimen was recovered from the Member 1 breccia during the 1948–52 operations at Swartkrans. It was discovered in 1966 amongst a number of supposedly non-hominid faunal remains by C. K. Brain, who performed some preliminary preparation on it. The description on the catalogue card reads, 'Fragment of maxilla with a slightly worn M^1 left and an erupting incisor?'

Prior to cleaning and restoration, this specimen consisted of a damaged left upper molar, the tip of a permanent lateral incisor and a small piece of what appeared to be the incisal edge of an incisor (Fig. 11). Also, a narrow, thin sheet of maxillary alveolar bone was present round the incisors, and at the back of the specimen the outline of what appeared to be part of an upper molar crown was visible in the matrix.

Preparation revealed a very badly damaged and fragmented LI^1 (Figs 12–13), much of the crown of the LI^2 (Fig. 12), the mesial part of what is here considered to be the LM^1 (Fig. 14), and the distal moiety of what is here believed to be a slightly worn Ldm^2 (Fig. 14).

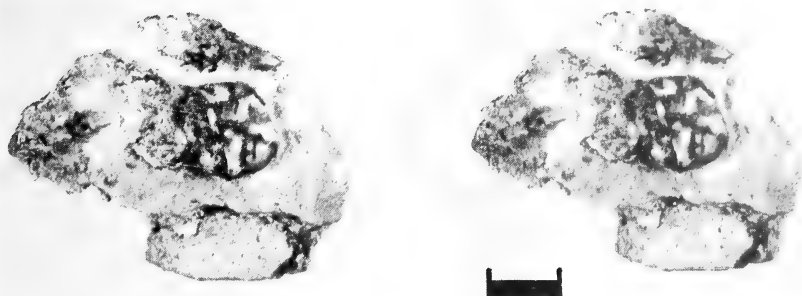


Fig. 11. Stereoview of SK 1595 prior to preparation. Compare with Figures 12-14.
Scale in cm.

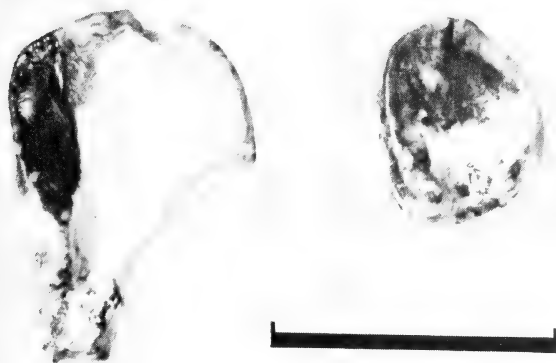


Fig. 12. Lingual view of LI¹ and LI² of SK 1595. Scale in cm.

Deciduous dentition (Fig. 14)

Maxillary second deciduous molar

The distal half or more of the crown of the left second deciduous molar is present. The mesial portion of the crown has been broken away along an uneven transverse line which courses through the middle of the protocone lingually, across the distal edge of the paracone buccally. Nothing of the radicular system remains.

It is evident that all four principal cusps were present originally, and it is probable that all were well developed. The metacone and hypocone are both well developed and they are nearly equal in size.

Occlusal wear is slight on the preserved part of the crown. The protocone is the most heavily worn cusp; it has been reduced in height more than the two distal cusps, and it shows a large, faintly convex enamel facet. The hypocone



Fig. 13. Buccal view of LI¹ of SK 1595.
Scale in cm.



Fig. 14. Occlusal view of the Ldm² and the mesial
portion of the LM¹ of SK 1595. Scale in cm.

displays a large, flattened enamel facet which slopes downwards mesiobuccally. The metacone shows the lightest wear of the three cusps, with only a small enamel facet. Dentine is not exposed. An interproximal attrition facet is not present on the distal surface of the crown.

Occlusally, the distal trigon crest is moderately thick but it is incised on its mesial and distal surfaces by a shallow groove. The distal marginal ridge is thick and complete. It is somewhat lower in its middle but is continuous high on to the distal aspect of the metacone. Four small cuspules are supported by this ridge; each cuspule is only faintly demarcated. The talon basin is relatively large and deep. A deep, narrow, longitudinal groove drains this basin near the middle of its mesial aspect, and this groove is continuous with the deep, narrow lingual groove between the protocone and hypocone.

The lingual surface over the hypocone is moderately convex occlusocervically and, although the cervical margin is damaged, it appears that a cervical enamel prominence was present. The lingual groove is relatively deep but narrow, and it courses vertically to the cervical margin. Approximately two-thirds of the way down the crown the groove is interrupted by a narrow (1,5 mm thick), horizontal enamel band.

Buccally, the surface is more swollen in appearance than the lingual. The face of the metacone is moderately convex occlusocervically. The buccal groove is rather deep and somewhat broader than the lingual. It continues vertically for about half of the crown height, where it ends abruptly in a deep pit. The pit is surrounded buccally by a thin, continuous enamel crest from the paracone to the metacone. Near the distal side of the metacone a short, shallow and narrow, vertical groove courses from the occlusal margin. This groove partially demarcates the most buccal of the distal cuspule (= distostyle) from the main body of the metacone. A few minute hypoplastic pits are shown on the mesiobuccal surface of the metacone, near the occlusal margin of this surface. Some hypoplastic mottling is present also on the distal surface of the crown.

The mesiodistal diameter of this crown is estimated to have been between 11,2 and 11,4 mm. The buccolingual diameter measured across the distal parts of paracone and protocone is some 12,5 mm, the original dimension is judged to have been perhaps another 0,2 mm greater.

	MD diameter (estimated)	BL diameter (as measured)	BL diameter (estimated)
Ldm ²	11,3 mm	12,5 mm	12,7 mm

Permanent dentition (Figs 12–14)

Maxillary central permanent incisor

The incomplete, isolated crown of the left maxillary incisor is represented. The crown, as preserved, was reconstructed from seven different fragments. Most of the lingual surface is missing, save for the mesial marginal ridge and a narrow bit of the incisodistal edge. The mesial surface is nearly complete, but

the cervical region is damaged. The buccal face is only slightly more complete than the lingual, where the mesial and incisal parts are present.

The crown is unworn and probably had not yet erupted—at least it had not yet reached occlusion—at the time of death.

The mesial corner of the incisal edge is squared off, with the incisal and mesial edges meeting at just slightly more than 90°. The distal corner is considerably more rounded than the mesial. The incisal edge appears gently curved mesiodistally. This edge is faintly scalloped, and the mesial part supports two broad, low mammelons.

Viewed from the buccal aspect, the crown appears to have been rather square in outline; its mesiodistal diameter is judged to have been only slightly less cervically than incisally. The buccal face is slightly convex incisocervically. Fine perikymatous lines are visible over much of the preserved surface.

Lingually, the mesial marginal ridge is only slightly developed. It is extremely thin and low incisally, and expands somewhat as it courses cervically.

	MD diameter (as measured)	BL diameter	Height
LI ¹	9,0 mm	—	—

Maxillary lateral permanent incisor

The left maxillary lateral incisor is represented by an isolated, somewhat damaged crown. The cervical region round the entire periphery of the crown has suffered enamel loss, this being heaviest distobuccally and lingually. The crown appears to be fully, or nearly fully, developed, and it is relatively small, especially when compared to the I¹.

The tip of the crown is surmounted by two small mammelon-like tubercles. Mesial to the tip, the occlusal edge courses only slightly downward to the mesial corner, which is rather strongly curved. The edge distal to the tubercles slopes cervically much more strongly, and the distal 'corner' is broadly rounded and lower than the mesial.

Viewed from the buccal aspect, the crown is almost square in general outline, but with the distal occlusal 'corner' reduced. The buccal surface is faintly convex occlusocervically and there is no evidence of either perikymatous or hypoplastic enamel.

Lingually, the cervical region is damaged; the presence, or otherwise, of the basal prominence cannot be determined. There is no evidence of the existence of lingual basal tubercles. Both the mesial and distal marginal ridges are faintly developed; they course round the periphery of the lingual face from the tip as thin, low enamel ridges. Towards the cervical margin, however, these ridges become slightly more prominent. The lingual surface is flat.

	MD diameter (as measured)	BL diameter	Height
LI ²	6,2 mm	—	—

Maxillary first permanent molar

The left molar is represented by the damaged mesial portion of the crown. This piece consists of much of the mesial surface, the lingual part of the paracone, the entire mesial marginal ridge, and the mesial part of the paracone. The preserved part of the crown is unworn and the tooth is judged to have been unerupted at the time of death.

The mesial marginal ridge is moderately thick and high. It is continuous, but is incised by two shallow grooves at the base of the tip of the paracone. A small cuspule (= epiconule) is demarcated by these grooves. The crest is expanded distally in its middle, and a small pit is situated atop it in this position. The fovea anterior is represented by an elongate, irregular and narrow transverse groove; it is broadest in front of the paracone. The protocone and paracone are separated by a relatively deep, broad groove by which the fovea anterior appears to be continuous with the trigon basin.

Measurements are not possible.

SPECIMEN SK 2147 (Fig. 15)

There is no catalogue card for this specimen. It was discovered in the collection, labelled as an isolated lower premolar; it is, in fact, an isolated, incomplete Ldm¹.

Prior to preparation, the crown sat atop, and was partially covered by, a small piece of typical 'Pink', or Member 1, Swartkrans breccia.

The specimen consists of the mesial two-thirds of a moderately worn crown, with much of the mesiobuccal root present. The distal part of the crown has been broken away along an irregular transverse line which cuts through the distal edge of the protocone, and through the lingual extent of the metacone where it turns sharply mesially to the posterior extent of the paracone. The crack extends directly lingually from this point along the plane occupied by the lingual developmental groove. Several narrow cracks traverse the protocone and the paracone. The cervical portion of the buccal surface is cracked, with considerable displacement of two rather large pieces of enamel. The mesial face of the crown has suffered slight enamel loss and cracking. A narrow horizontal crack traverses the mesial surface of the mesiobuccal root, and the tip of the lingual part of this root has been damaged near its apex.

The occlusal outline of the crown cannot be determined. The protocone is a very large cusp; the paracone is well developed also, but considerably smaller than the protocone. Mesial to the paracone a large mesiostyle (= parastyle or paraconule) is present. The mesiostyle is separated from the paracone by a relatively deep, broad groove.

Occlusal wear is moderate. The protocone has been reduced considerably in height, with a large, nearly flat and slightly lingually sloping enamel facet. A large, elongate and ovoid-shaped, concave dentine exposure is present in the middle of the protocone. The buccal side of the crown is less heavily worn; the

paracone, mesiostyle and mesial marginal ridge all show enamel wear. A small island of dentine is exposed on the tip of the paracone.

Interproximal attrition, at least mesially, appears to have been moderate. A large, slightly concave facet for the d^c is present at the buccal extremity of the mesial surface, it measures 2,8 mm buccolingually and 2,5 mm in height.

Occlusally (Fig. 15), the mesial marginal ridge is well developed. It is thick and relatively high, and extends continuously from the mesiostyle to the mesiolingual aspect of the protocone. The fovea anterior is represented by a



Fig. 15. Occlusal view of SK 2147 Ldm¹.
Scale in cm.

relatively deep, broad groove which is continuous with the incision between the paracone and mesiostyle. The fovea is enclosed distally by a high, moderately thick enamel crest between the anterior part of the paracone and the protocone. The trigon basin is represented by a relatively deep and broad λ -shaped groove. The tines of the λ encompass part of the buccal aspect of the protocone between this cusp and the paracone and metacone. The stem of the λ has been damaged, but it is evident that it represented the buccal developmental groove between the paracone and metacone.

The lingual surface of the protocone is slightly convex occlusocervically and a slight cervical enamel prominence is shown.

The cervical portion of the buccal surface has been damaged, but this portion was seemingly less convex than the lingual face, with a slight cervical enamel prominence. The occlusal two-thirds of the buccal face is relatively flat. The buccal groove is missing. A faint groove courses vertically for a short distance from the occlusal incision between the paracone and the mesiostyle. It is apparent that there was no tuberculum molare over the mesiocervical aspect of the buccal surface.

	MD diameter	BL diameter (as measured)	BL diameter (corrected)
Ldm ¹	—	9,8 mm	10,0 mm

The mesiobuccal root has a flattened, ovoid outline in cross-section; it is expanded buccolingually and compressed mesiodistally. The long axis of the root, in cross-section, runs slightly mesiobuccally-distolingually. The buccolingual diameter measures some 5,3 mm and the mesiodistal some 3,9 mm at the cervical margin. The root is relatively straight, and it courses rather markedly mesially from the cervical line to its tip. It diverges buccally somewhat. This root is estimated to have been approximately 8,5 mm long.

DISCUSSION

Four specimens representing the jaws and/or teeth of some three juvenile hominid individuals from Swartkrans have been prepared and described in detail. The remains are all derived from Member 1 breccia. These specimens have added a number of deciduous and permanent teeth to the already sizeable collection from this site.

Robinson (1956) referred one of these specimens (SK 839) to *Paranthropus robustus*. Wallace (1972) suggested that SK 839 and SK 852 represent a single individual, and he included this composite in his hypodigm of *Australopithecus robustus* from Swartkrans. The results of the present study support Wallace's suggestion that SK 839 and SK 852 belonged to a single individual. SK 1595 was also referred to *A. robustus* by Wallace (1972) on the basis of the occlusal wear pattern exhibited by the dm².

The fourth specimen, SK 2147, was catalogued as an isolated permanent premolar. The author considers this tooth to be a left dm¹, and as such it represents, to date, the second specimen of this tooth found at Swartkrans. The other dm¹, SK 91, has been referred by both Robinson (1956) and Wallace (1972) to the 'robust' australopithecine taxon. The morphology shown by SK 2147 is similar to that evinced by SK 91, and the dm¹ of SK 2147 is also referred to the Swartkrans 'robust' australopithecine taxon.

An analysis of the morphological and metrical data available for the collection of deciduous and permanent teeth from Swartkrans is beyond the scope of the present paper and will be presented elsewhere.

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Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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F. E. GRINE

DESCRIPTION OF SOME JUVENILE
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FROM SWARTKRANS, TRANSVAAL

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(continued inside back cover)

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DINOCEPHALIA TYPE MATERIAL
IN THE SOUTH AFRICAN MUSEUM
(REPTILIA, THERAPSIDA)

By

J. A. VAN DEN HEEVER

&

F. E. GRINE

Cape Town Kaapstad

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DINOCEPHALIA TYPE MATERIAL IN THE SOUTH AFRICAN MUSEUM (REPTILIA, THERAPSIDA)

By

J.A. VAN DEN HEEVER*

&

F.E. GRINE

South African Museum, Cape Town

[MS accepted 14 May 1981]

ABSTRACT

Brief statements on the preservation of the dinocephalian type specimens, the localities from which they were recovered, and the collectors responsible are given. The original generic and/or specific diagnoses are reproduced. All relevant references to each specimen are listed, together with pertinent comments.

CONTENTS

	PAGE
Introduction	73
Type material	74
Family Anteosauridae	74
Family Titanosuchidae	85
Family Tapinocephalidae	98
Subfamily Tapinocephalinae	98
Subfamily Struthiocephalinae	99
Subfamily Riebeeckosaurinae	104
Subfamily Moschopinae	106
Family Styracocephalidae	111
Acknowledgements	112
References	112

INTRODUCTION

The infra-order Dinocephalia (assuming that this group is monophyletic) represents a Middle Permian radiation of carnivorous and herbivorous therapsids. In the *Tapinocephalus* Zone (Kitching 1977) sediments of the Beaufort Group, Cape Province, South Africa, the dinocephalians form a substantial part of the dominant therapsid fauna. It is commonly held that the South African dinocephalians are derived from earlier Russian therapsids (Olson 1962; Boonstra 1969; Tatarinov 1974, 1976).

Since the South African Museum houses the largest collection of dinocephalian type specimens, it was felt that a comprehensive list of this material would serve a useful purpose. The collection contains some forty-four holotype

* The order of authorship was decided by the flip of a coin.

and paratype specimens and, in order to present this list of material in a clear manner, Boonstra's (1969) familial and subfamilial classifications have been utilized.

The generic and specific diagnoses included in this paper are taken from the original diagnosis of each taxon. Those that have been indicated clearly as diagnoses are reproduced verbatim. In some instances, where the taxonomic diagnosis was not clearly separated from the descriptive text, the present authors have scrutinized the description in order to determine which features were considered by the original author to be diagnostic. However, in all cases the terminology remains that of the original author.

Most of the localities are represented by farm names, spelt in a variety of ways by different workers. In order to avoid confusion, the authors have followed Kitching (1977) in the spelling of locality names.

TYPE MATERIAL

Family *Anteosauridae*

Anteosaurus abeli Boonstra, 1952

Holotype

SAM-11296

Material

Fairly complete skull and lower jaw which have been distorted slightly by shear.

Locality

Kruisrivier, Sutherland.

Collected

Boonstra and Laurenson, 1937.

Generic diagnosis

See Watson (1921) for diagnosis of *Anteosaurus*.

Specific diagnosis

Skull large and massive; postorbital boss less massive than in genotype [*sic*]; jugal boss low to very prominent; bone thickened around pineal foramen but does not form a clear, circular boss; frontals strongly swollen; tooth-bearing palatine boss semilunate; premaxillary edge slopes upward in contrast to genotype [*sic*]; incisors very long with only some showing slight indication of lingual step; premaxillae greatly swollen dorsally and clearly demarcated from maxillae; squamosal moderately flared laterally; dentary strong and very massive (after Boonstra 1952e: 150).

References

- Boonstra 1948: 40 (fig.).
Boonstra 1952e: 150–151.
Boonstra 1953a: 26, pl. 1.
Boonstra 1954a: 109, 112–114, 124–125, 144, figs 1–2.
Haughton & Brink 1955: 42.
Piveteau 1961a: 84, fig. 11.

Comments

Boonstra (1969) regarded *Anteosaurus abeli* as a junior synonym of *Anteosaurus magnificus*.

Paratype

SAM-340

Material

Good skull and part of lower jaw which have been distorted by shear.

Locality

Leeurivier, Beaufort West.

Collected

Haughton, 1916.

References

- Boonstra 1952e: 150.
Boonstra 1953a: pl. 3.
Boonstra 1954a: 108, 112–113, 124, 130, 144, fig. 6.

Comments

An isolated symphysis labelled SAM-4340 does not belong to this individual. There are several unlabelled fragments associated with the specimen which do not appear to belong to it.

Paratype

SAM-5621

Material

Incomplete, fragmentary skull consisting of part of snout and a portion of cranial roof.

Locality

Leeurivier, Beaufort West.

Collected

Haughton, 1916.

References

Boonstra 1952*e*: 150.

Boonstra 1954*a*: 108, 131, 144.

Paratype

SAM-9123

Material

Weathered and sectioned skull lacking lower jaw; two vertebrae.

Locality

Voëlfontein, Prince Albert.

Collected

Boonstra, 1929.

References

Boonstra 1952*e*: 150.

Boonstra 1954*a*: 108, 131, 144.

Boonstra 1962: 97–98; fig. 33.

Paratype

SAM-11302

Material

Fairly complete but weathered skull with part of lower jaw.

Locality

Buffelsvlei, Beaufort West.

Collected

Boonstra, 1938.

References

Boonstra 1952*e*: 150.

Boonstra 1954*a*: 134–135, 144.

Comments

Boonstra (1954*a*) placed this specimen in the hypodigm of *Anteosaurus crassifrons*.

Paratype

SAM-11929

Material

Imperfect, weathered skull.

Locality

See comments.

Collected

See comments.

References

Boonstra 1952e: 150.

Boonstra 1954a: 109, 135, 144.

Comments

The locality is questionable. In the museum catalogue it is given as 'unknown, probably near Abrahamskraal, Prince Albert'. Boonstra (1954a: 109) gave the locality as Kruisvlei, Beaufort West, but later in the same paper he (1954a: 135) referred to the locality as Abrahamskraal, Prince Albert. The museum catalogue records the collector as 'unknown'; Boonstra (1954a: 109) stated that he collected it. Boonstra (1954a) placed this specimen in the hypodigm of *Anteosaurus crassifrons*.

Anteosaurus acutirostris Boonstra, 1954

Holotype

SAM-9329

Material

Nearly complete skull and lower jaw.

Locality

Kruisvlei, Beaufort West.

Collected

Boonstra, 1929.

Generic diagnosis

See Watson (1921) for diagnosis of *Anteosaurus*.

Specific diagnosis

Skull large, maximum length of 675 mm. Snout long, high, narrow, and light. Intersquamosal width great (480? mm). Postfrontal boss huge and pro-

minent. Jugal boss massive, angular boss massive. Fronto-naso-prefrontal swelling very strong with distinct step on to the anterior nasal surface and laterally slightly overhanging the sides of the skull. Pineal boss low with rounded edges extending to the occipital edge. Fairly strong upward inclination of premaxillary edge. Occiput high, fairly wide, very deeply concave with sharp and great posterior sweep of temporal arches; upper part of temporal fossa roomy anteroposteriorly. Temporal arch rises above plane of intertemporal surface. Palate apparently long and narrow. Basis cranii fairly long. Exoccipitals fused with basioccipital to form rounded condyle, which is visible beyond occipital edge in dorsal view. On both sides 4 upper and 4 lower incisors, 1 canine, 5? postcanines. (After Boonstra 1954a: 131–132.)

References

- Boonstra 1952e: 150.
Boonstra 1953a: pl. 2.
Boonstra 1954a: 108, 113, 131–133, 144, fig. 10.
Haughton & Brink 1955: 42.

Comments

Boonstra (1969) regarded *Anteosaurus acutirostris* as a junior synonym of *Anteosaurus magnificus*.

Anteosaurus crassifrons Boonstra, 1954

Holotype

SAM-11946

Material

Good skull distorted by shear.

Locality

Buffelsvlei, Beaufort West.

Collected

Boonstra and Marais, 1951.

Generic diagnosis

See Watson (1921) for diagnosis of *Anteosaurus*.

Specific diagnosis

Skull large but short and squat; maximum length 570 mm. Snout short, high and very wide. Intersquamosal width fairly small (330? mm). Postfrontal boss fairly massive and prominent. Jugal boss massive. Fronto-naso-prefrontal swelling very massive with very distinct step on to anterior nasal surface and

laterally strongly overhanging sides of skull. Pineal boss rounded, large and extending on to frontal. Very sharp inclination of premaxillary edge. Occiput high, fairly wide, deeply concave, with great posterior sweep of temporal arches. Upper part of temporal fossa roomy in anteroposterior direction. Temporal arch not rising above plane of intertemporal surface. Palate very short with massive lateral pterygoid flanges. Basis cranii short, with short basisphenoid. Exoccipitals fused with basi-occipital to form rounded condyle. In both premaxillae teeth not preserved but five matrix-filled alveoli shown; in both maxillae five postcanine roots of greatly varying diameter preserved, numbers 2 and 5 much smaller than other three. (After Boonstra 1954a: 133–134.)

References

- Boonstra 1954a: 109, 113, 133–134, 144, figs 11–13.
Haughton & Brink 1955: 42.

Comments

Boonstra (1969) regarded *Anteosaurus crassifrons* as a junior synonym of *Anteosaurus magnificus*.

Anteosaurus cruentus Boonstra, 1954

Holotype

SAM-11694

Material

Reasonably complete skull without lower jaw.

Locality

Koringplaas, Laingsburg.

Collected

Boonstra and Du Plessis, 1946.

Generic diagnosis

See Watson (1921) for diagnosis of *Anteosaurus*.

Specific Diagnosis

Skull moderately large, maximum length 565 mm. Snout long, narrow and fairly low. Intersquamosal width not great (360 mm). Postfrontal boss fairly strong and prominent. No jugal boss. Fronto-naso-prefrontal swelling small, passing evenly on to anterior nasal surface. Pineal boss prominent, with sharp circular border, situated very near occipital edge. Sharp upward inclination of premaxillary edge. Occiput high and fairly broad, very deeply concave with

great posterior sweep of temporal arch. Upper part of temporal fossa roomy anteroposteriorly; temporal arch not rising above very narrow intertemporal surface. Palate long, with fairly robust lateral pterygoid flanges. Basis cranii long, but basisphenoid short. Exoccipitals form large part of dorsolateral corners of condyle. Alveolar face of premaxilla shows matrix-filled groove divided in its posterior part by distinct alveoli; appears to have been room for 5 incisors when fully developed. On right side canine root followed by roots of 6 postcanines, but on left only 4 roots with a possible fifth visible. (After Boonstra 1954a: 139–140.)

References

Boonstra 1953a: 26, pl. 6.

Boonstra 1954a: 109, 112, 114, 124, 139–141, 144, figs 17–20.

Haughton & Brink 1955: 42.

Comments

Boonstra (1953a) referred this specimen to *A. minor*. Boonstra (1969) regarded *Anteosaurus cruentus* as a junior synonym of *A. magnificus*.

Anteosaurus levops Boonstra, 1954

Holotype

SAM-11492

Material

Badly weathered, incomplete skull without lower jaw.

Locality

Mynhardtskraal, Beaufort West.

Collected

Boonstra and Bothma, 1940.

Generic diagnosis

See Watson (1921) for diagnosis of *Anteosaurus*.

Specific diagnosis

Skull fairly small, maximum length 485 mm. Snout fairly short, lightly built, narrow and low. Intersquamosal width relatively large (415 mm). Post-frontal boss strong and prominent. No jugal boss. Fronto-naso-prefrontal swelling strong, with distinct step on to anterior nasal surface and laterally slightly overhanging sides of skull. Pineal boss apparently prominent, reaching occipital edge. Upward inclination of premaxillary edge moderate. Occipital fairly low and broad, deeply concave, not vertical; strong posterolateral sweep

of temporal arches. Upper part of temporal fossa shortened in anteroposterior direction; temporal arch rising above plane of narrow intertemporal surface. Palate long and narrow. Basis cranii fairly short. In right premaxilla parts of crowns of 3 incisors preserved, but on left there is a matrix-filled groove with no sign of teeth. (After Boonstra 1954a: 141–142.)

References

- Boonstra 1953a: 26.
Boonstra 1954a: 109, 141–142, 144, fig. 21.
Haughton & Brink 1955: 43.

Comments

Boonstra (1953a) considered this skull to be a referred specimen of *A. minor*. Boonstra (1969) regarded *A. Levops* as a junior synonym of *A. magnificus*.

Anteosaurus laticeps Boonstra 1954

Holotype

SAM-11592

Material

Incomplete skull with only ventral and occipital surfaces preserved.

Locality

Dikbome, Laingsburg.

Collected

Boonstra and Du Plessis, 1942.

Generic diagnosis

See Watson (1921) for diagnosis of *Anteosaurus*.

Specific diagnosis

Skull large, maximum length 645? mm. Snout short and very broad. Intersquamosal width great (522 mm). Occiput low and very broad, shallowly concave; sweep of temporal arches mostly lateral. Palate long and very broad with only moderately strong lateral pterygoidal flanges. Basis cranii short, with very short basisphenoid. Exoccipitals form much of dorsolateral corners of condyle. Canines very strong and slightly recurved. In right maxilla, stumps of 5 postcanines can be made out whereas on left 5 teeth are preserved with the probability of another 2, making a total of 7. Postcanines bluntly conical, but linguolabially compressed with crowns thus oval in cross-section (16 x 11 x 7 mm). (After Boonstra 1954a: 138–139.)

References

- Boonstra 1952e: 150.
Boonstra 1953a: 22.
Boonstra 1954a: 109, 138–139, 144, fig. 16.
Haughton & Brink 1955: 42.

Comments

Boonstra (1952e) made this specimen a paratype of *A. abeli*. Later he (1953a) appears to infer that he considers it to be a specimen of *Jonkeria* sp. Boonstra (1969) regarded *A. laticeps* as a junior synonym of *A. magnificus*.

Anteosaurus major Boonstra, 1954

Holotype

SAM-11293

Material

Good skull, dorsoventrally compressed, lacking snout.

Locality

Boesmansrivier, Beaufort West.

Collected

Boonstra, 1937.

Generic diagnosis

See Watson (1921) for diagnosis of *Anteosaurus*.

Specific diagnosis

Skull very large, maximum length 805? mm. Snout long, fairly broad and high. Intersquamosal width very great (612 mm). Postfrontal boss only moderately strong and not very prominent, with postorbital forming posterolateral part. Low and weak jugal boss. Fronto-naso-prefrontal boss moderate, confluent with anterior nasal surface. Pineal boss low, with rounded edges, situated some distance from occipital edge. Occiput low and broad, moderately deeply concave. Sweep of temporal arches more lateral than posterior and upper part of temporal fossa roomy anteroposteriorly. Temporal arch rises above level of intertemporal surface. Palate fairly long and broad, with strong and deep lateral pterygoidal flanges but not so massive as in *A. crassifrons*. Basis cranii long and basisphenoid much longer than in any of the other species. Exoccipitals from dorsolateral corners of condyle. (After Boonstra 1954a: 136–138.)

References

- Boonstra 1952e: 150.
Boonstra 1953a: pls 4–5.

Boonstra 1954a: 109, 120, 136–138, 144, figs 14–15.

Haughton & Brink 1955: 42.

Comments

Boonstra (1952e) referred to this specimen as a paratype of *A. abeli*.
Boonstra (1969) synonymized this taxon with *Anteosaurus magnificus*.

Micranteosaurus parvus Boonstra, 1954

Holotype

SAM-4323

Material

Anterior part of snout, lower jaw, manus, pes, femur, fibula, proximal part of humerus, radius, coracoid, caudal vertebra.

Locality

Merweville commonage, Beaufort West.

Collected

Haughton, 1917.

Generic diagnosis

Anteosaurid of very small size (after Boonstra 1954b: 156).

Specific diagnosis

As for genus.

References

Boonstra 1954b: 149–156, figs 1–4, pl. 18.

Boonstra 1955b: 200, 320–321.

Haughton & Brink 1955: 45.

Von Huene 1956: 287.

Piveteau 1961a: 85.

Orlov 1964: 254.

Boonstra 1966: 14, 17–18, 23–25, figs 3, 10.

Boonstra 1969: 33.

Comments

Boonstra (1969) regarded this specimen as a juvenile *Anteosaurus magnificus*.

Paranteosaurus primus Boonstra, 1954

Holotype

SAM-11485

Material

Partial, fragmented skull, proximal end of femur, vertebrae.

Locality

Mynhardtskraal, Beaufort West.

Collected

Boonstra, 1940.

Generic diagnosis

'A medium-sized Anteosaurid [sic] (max. length probably about 570 mm), with small postfrontal not extending posteriorly, lightly built postorbital bar, without any sign of a boss-like development in the upper part of the postorbital bar, dental formula I.3?-4?, C.1, P.C.5' (Boonstra 1954c: 159).

Specific diagnosis

As for genus.

References

- Boonstra 1952e: 150.
Boonstra 1954c: 157-159.
Boonstra 1955b: 320, fig. 102e.
Haughton & Brink 1955: 45.
Piveteau 1961a: 85.
Boonstra 1963a: 177, fig. 8G.
Boonstra 1963b: 200, fig. 4A.
Orlov 1964: 254.
Boonstra 1969: 33, 35, 55.

Eccasaurus priscus Broom, 1909

Holotype

SAM-915

Material

Humerus, two imperfect femora, fibula, distal end of tibia, occipital fragment, tooth, nine weathered vertebrae, rib fragments, nine additional badly preserved fragments.

Locality

Sandvlakte, Prince Albert.

Collected

Presented by Cairncross.

Generic diagnosis

Humerus with well-developed deltopectoral ridge which does not continue to head (after Broom 1909a: 276).

Specific diagnosis

As for genus.

References

- Broom 1909a: 276–277.
Gregory 1926: 235.
Broom 1932: 45, fig. 3c-d.
Boonstra 1955b: 188, 321–322, figs 105–106, 107a.
Haughton & Brink 1955: 47.
Romer 1966: 373.
Boonstra 1969: 33.

Comments

Broom (1909a) considered the humerus to be most similar to that of *Procolophon*, but felt *Eccasaurus* to be a primitive diaptosaurian which ‘probably belongs to a new suborder’. In 1932 he expressed the opinion that *Eccasaurus* is undoubtedly a tapinocephaloid and noted that its humerus resembles, in both morphology and size, that of *Moschops*. Boonstra (1955b) considered *Eccasaurus* to be an anteosaurid, while Romer (1966) placed the genus in the family Tapinocephalidae. Boonstra (1969) regarded the taxon to be determinable only to family.

Family Titanosuchidae

Archaeosuchus cairncrossi Broom, 1905

Holotype

SAM-916

Material

Maxilla, weathered and incomplete (side questionable).

Locality

Sandvlakte, Prince Albert.

Collected

Cairncross.

Generic diagnosis

Broom (1905) did not give a diagnosis but commented that the canine looked titanosuchian. Broom (1932: 18) stated that: ‘The canine is remarkable

in having a posterior ledge. The molars are relatively small, short conical teeth.'

Specific diagnosis

As for genus.

References

- Broom 1905: 333–335.
Broom 1909*b*: 287.
Broom 1932: 18, fig. 3J.
Boonstra 1953*a*: 28.
Haughton & Brink 1955: 46.

Comments

Broom (1905) provisionally placed this taxon in the Therocephalia, but in 1909 he put it in the Dinocephalia. Broom (1932) commented that it was perhaps representative of a 'pre-dinocephalian group'. Boonstra (1953*a*) transferred this specimen to *Titanosuchus* and questioned its specific validity. Boonstra (1969) noted that the specimen was so poor that it must be regarded as a *nomen dubium*.

Dinosphageus haughtoni Broom, 1929

Holotype

SAM-4343

Material

Humeri, ilia, good skull without lower jaw, scapula, cleithrum, ulna, ischium, femur, ?fibula, coracoids and vertebrae.

Locality

Welgemoed, Leeu-Gamka, Prince Albert.

Collected

Haughton, 1916.

Generic diagnosis

Vomers form marked median ridge on their posterior two-thirds. Pterygoids project much less downward than in *Jonkeria*. Upper half of humerus little more in plane of lower half than is the case in humerus of *Jonkeria* and, as a result, on side view the deltopectoral crest appears smaller, but this may be due to crushing. Upper portion of ilium relatively smaller than in *Jonkeria*. (After Broom 1929: 31.)

Specific diagnosis

As for genus.

References

- Broom 1929: 31, figs 17–19.
Broom 1932: 29, fig. 7D.
Boonstra 1953a: 27.
Boonstra 1955b: 189, 287–293, figs 75–80.
Haughton & Brink 1955: 44.
Boonstra 1962: 78–80, fig. 18.
Boonstra 1965b: 263, fig. 9.
Boonstra 1969: 37.

Comments

Broom (1932) emended the diagnosis. Boonstra (1953a) transferred the species to *Jonkeria*. No mention is made in the literature of vertebrae belonging to the specimen but several vertebrae were found bearing the number SAM-4343 and probably belong to the specimen.

Jonkeria koupensis Boonstra, 1955

Holotype

SAM-9004

Material

Pelvis lacking ischia; distal two-thirds of ulna.

Locality

Klein Koedoeskop, Beaufort West.

Collected

Boonstra, 1929

Generic diagnosis

See Van Hoepen (1916) for diagnosis of *Jonkeria*.

Specific diagnosis

Pubo-ischiadic plate probably short (83 per cent of height as reconstructed); supra-acetabular part of ilium high (264 mm) and anteroposterior length of iliac blade very short (282 mm), so that height is 93 per cent of length; anterior iliac process fairly short, but appears shorter than it really is because of strong anterolateral eversion and it is fairly high; posterior process short and fairly low, with posteroventral edge moderately strongly folded over to form a fairly strong iliofibularis ridge on outer face; this ridge is directed obliquely upward, with its upper end not strongly bulbously thickened; a slight groove on the inner face of the everted anterior iliac process indicates attachment of rib anterior to main sacral rib; anteroposteriorly the outer face of iliac blade deeply

concave. Anteroventral edge of pubis strongly everted, with tuberculum pubis confluent with thickened part of anteroventral edge, which stretches to median line where the pubes meet but do not form a real symphysis. Ulna massive with dorsal lip of sigmoid face developed into massive swelling in its pre-axial part. (After Boonstra 1955b: 301.)

References

Boonstra 1955b: 301, fig. 87.

Boonstra 1969: 38.

Jonkeria parva Boonstra, 1955

Holotype

SAM-9149

Material

Well-preserved right humerus.

Locality

Saairivier, Prince Albert.

Collected

Boonstra, 1929.

Generic diagnosis

See Van Hoepen (1916) for diagnosis of *Jonkeria*.

Specific diagnosis

Smallest *Jonkeria* humerus known; length only 312 mm, but it is a very massive element with both proximal (222 mm) and distal (252 mm) ends very greatly expanded; shaft very short and bone greatly constricted in waist; diameters of shaft 84 x 78 mm; deltopectoral crest fairly short and terminates very far proximal of the plane in which entepicondylar foramen lies; it has a very massive ventral edge, and terminates as a very thick knob. Caput weak and its face strap-like, but it forms the most proximal part of the bone; processus lateralis lies more distal than the caput; processus medialis, as in all *Jonkerias* [sic], lies well distal of caput; capitellum very massive and extends very far proximally along ventral face, with its proximal border lying in a plane proximal to that in which the entepicondylar foramen lies; posterior to capitellum there is a deep groove in which the coronoid process moved when the ulna was flexed; twist of shaft great (30°); lateromedial line distinct with large, mound-like muscle scar on dorsal surface of shaft; anterior dorsoventral line very strong and forms prominent ridge; entepicondyle strongly developed to form a greatly outflaring, thick sheet of bone; ventral opening of entepicon-

dylar foramen oval and lies well postaxially, near edge of bone; ectepicondyle developed as a greatly flaring thin sheet of bone penetrated in its thinner part near edge by small, round ectepicondylar foramen. (After Boonstra 1955b: 303.)

References

- Boonstra 1955b: 192, 303, fig. 89.
Boonstra 1969: 38.

Jonkeria rossouwi Boonstra, 1955

Holotype

SAM-5014

Material

Left scapula, incomplete precoracoid and coracoid, imperfect interclavicle, left humerus, left ulna, left radius, right ilium, left femur, left tibia, left fibula.

Locality

Abrahamskraal, Prince Albert.

Collected

Haughton per Van der Byl.

Generic diagnosis

See Van Hoepen (1916) for diagnosis of *Jonkeria*.

Specific diagnosis

Pectoral girdle fairly large and fairly massive; scapula fairly low (height 552 mm) and upper part of blade greatly expanded (width 324 mm), tricipital bulge very prominent, supraglenoidal edge forms strong raised rim; internal opening of supracoracoid foramen opens into deep subscapular groove; glenoidal facet of scapula faces ventroposteriorly but not externally; precoracoid long but low, foramen pierces bone very obliquely. Coracoid small but massive, with large glenoidal facet facing well externally.

Interclavicle massive but short (480? mm) with stem wide posteriorly and with a narrowed waist anteriorly; anterior spatulate end curves upwards very sharply and has deep groove on outer anterolateral face for reception of posteroventral edge of clavicle; on dorsal surface of stem there is a strong medial ridge against which the precoracoids abut.

Humerus fairly short (378 mm in length), but massive with greatly expanded proximal (330 mm) and distal (276? mm) ends; shaft very short, thick and broad (132 x 84 mm); deltopectoral crest very long and nearly reaches plane in

which entepicondylar foramen lies; caput broadly oval; processus lateralis lies well proximally, in same plane as caput, whereas processus medialis lies well distally; capitellum fairly massive and extends well along ventral face and nearly reaches plane of entepicondylar foramen; 'twist' on shaft fairly small (15°); lateromedial line fairly strong with muscle scars on dorsal surface of shaft; anterior dorsoventral line well developed; entepicondyle strong with ventral opening of foramen large and nearly round; ectepicondyle forms thick flange pierced by small foramen situated well away from edge of bone.

Ulna pathological but the normal condition would appear to have had a more slender shaft and weaker coronoid process than in other known species of *Jonkeria*.

Radius (length 312 mm) with flange on proximopostaxial corner weak.

Supra-acetabular part of ilium high (288 mm) and relatively short (336 mm) so that height is 87 per cent of length; anterior iliac process relatively short, but fairly high and strongly everted; posterior process short and fairly low, with posteroventral edge folded over strongly to form strong vertical ridge, which is dorsally strongly bulbous, and projects strongly laterally; on inner face of anterior iliac process no distinct facet is preserved for attachment of rib lying anterior to main sacral rib.

Femur fairly long (504 mm); fairly broad over external trochanter (264 mm), which is not separated by notch from proximal face; caput fairly thick (114 mm) and directed much preaxially; shaft broad but flat (156 x 84 mm); femorotibialis ridge fairly strong; distal facets of femur small and directed much distally, especially the entepicondyle which lies far distally.

Tibia fairly robust (length 300 mm); proximal face inclined much postaxially to correspond with the distally situated postaxial facet of femur.

Fibula fairly slender and long (330 mm). (All after Boonstra 1955b: 303–305, 309.)

References

Broom 1929: 27–29, figs 15–16.

Boonstra 1955b: 303–305, 309, figs 90–97.

Comments

Broom (1929) referred to this specimen as *Jonkeria* sp. and merely noted the presence of other elements.

Parascapanodon avifontis Boonstra, 1955

Holotype

SAM-9127

Material

Good precoracoid, clavicle, fibula and femur associated with parts of a large skull.

Locality

Voëlfontein, Prince Albert.

Collected

Boonstra, 1929.

Generic diagnosis

'The generic characters of the pectoral girdle are as described for the family [Titanosuchidae]' (Boonstra 1955b: 274), i.e. pectoral girdle large and massive . . . length of coracoidal plate 62–67 per cent of height. Scapula high and upper end of blade broad to very broad; scapular head of triceps attached to sharp ridge or prominent mound. Precoracoid large and massive, coracoid of medium size but massive. Clavicle large and mediolaterally flattened with expanded dorsal and ventral ends but waist not greatly constricted, ventral spatulate end curves inward to fit over outer face of upturned anterolateral corner of interclavicle; dorsal anterior end greatly thickened and produced dorsally as a short, strong process which fits into groove on lower end of cleithrum. Interclavicle large and massive, lateral horns with thickened postero-lateral edges, anterior to which there is a fairly deep groove to house ventro-posterior edge of spatulate end of clavicle.

Humerus very large and massive, length 575 mm and ends greatly expanded (proximal 310? mm, distal 312 mm); shaft fairly long but very robust (144 x 142 mm); deltopectoral crest long but terminates well proximal of plane in which entepicondylar foramen lies; caput very massive but short; processus medialis lies just a little distally of a plane in which caput lies, capitellum very strong and massive and extends far along ventral face but does not reach plane of entepicondylar foramen; twist on shaft large (40°); lateromedial line strong with massive swelling on dorsal surface of shaft, both epicondyles strongly developed; ventral opening of entepicondylar foramen large and broadly oval, ectepicondylar foramen small and situated well away from edge of bone.

Ulna large and massive (length 372 mm, width over coronoid process 200 mm); sigmoid face long, with ventral part broadly rounded; coronoid process situated far distally and shaft massive, broad and short.

Radius long, robust (length 294 mm) with strong proximopostaxial flange.

Femur very long and massive (length 595 mm); very broad over external trochanter (300 mm); pre-axial face deeply concave, with caput much pre-axially directed and massive (diams 215 x 167 mm); external trochanter indistinctly separated by notch from proximal face; shaft fairly long and broad (breadth 150 mm); wide over massive distal facets; area of origin of femorotibialis forms strong bulging ridge.

Tibia large and massive (length 330–355 mm); cnemial eminence very massive and continued distally as strong ridge, with deep groove lying post-axially.

Fibula large and stout (length 330–345 mm). (All after Boonstra 1955b: 266–267, 274, 276.)

Specific diagnosis

As for genus.

References

Boonstra 1955b: 266–267, 274, 276, 278, figs 63–66.

Boonstra 1962: 69, figs 10, 39A.

Comments

The skull is not described, illustrated or considered in the diagnosis. Boonstra (1969) considered all characters described under the names *Titanosuchus*, *Scapanodon*, and *Parascapanodon* as diagnostic of the form *Titanosuchus ferox*.

Paratype

SAM-9106

Material

Incomplete scapula, coracoid and precoracoid.

Locality

Veldmansrivier, Prince Albert.

Collected

Boonstra, 1929.

References

Boonstra 1955b: 278, fig. 67.

Paratype

SAM-9163

Material

Good fibula and fair ulna.

Locality

Wakkerstroom (part of Wolwefontein), Prince Albert.

Collected

Boonstra, 1929.

References

Boonstra 1955b: 280, fig. 70a-e.

Paratype

SAM-11299

Material

Right tibia and right radius.

Locality

Boesmansrivier, Beaufort West.

Collected

Boonstra, 1938.

References

Boonstra 1955b: 281, fig. 71a-f.

Paratype

SAM-11488

Material

Interclavicle, precoracoids, coracoid, right tibia, right fibula.

Locality

Mynhardtskraal, Beaufort West.

Collected

Boonstra, 1940.

References

Boonstra 1955b: 278, figs 68, 69a-f.

Comments

According to the museum catalogue, the locality is Mynhardtskraal, Beaufort West. Boonstra (1955) recorded the locality as Voëlfontein, Prince Albert. On both the tibia and fibula the number SAM-9123 has been scratched out. SAM-9123 is the paratype of *A. abeli*, a skull from Voëlfontein, Prince Albert. It would appear, therefore, that Mynhardtskraal is the correct locality.

Paratype

SAM-11881

Material

Humerus.

Locality

Bloukrans, Prince Albert.

Collected

Boonstra, 1948.

References

Boonstra 1955b: 284, fig. 72.

Scapanodon duplessisi Broom, 1904

Holotype

SAM-769

Material

Three lower jaw fragments.

Locality

Seekoeigat, Prince Albert.

Collected

Presented by Du Plessis.

Generic diagnosis

Two fairly large incisors, very large canine and (at least) eleven molars. Molars considerably smaller and much flatter than in *Titanosuchus*. Molars two-thirds of size of *Titanosuchus*. Section of deeper part of molar root narrow oval and becomes flatter as approaches alveolar margin. Supra-alveolar part of tooth has fair-sized root apparently devoid of enamel, with edges moderately parallel. In crown the flattening continued to even greater extent. Thickest part of crown not more than 2,0 mm thick and from centre it thins off towards edges. Tooth strengthened by being slightly concavoconvex. External surface not grooved though slightly uneven, no serrations visible at edges. Enamel very thin (about 0,15 mm). (After Broom 1904: 182-183.)

Specific diagnosis

As for genus.

References

Broom 1904: 182-183.

Broom 1923: 663.

Broom 1932: 30.

Boonstra 1953a: 25, 28.

Haughton & Brink 1955: 46.

Boonstra 1969: 35.

Comments

Broom (1904) described two of the fragments, which belong to the same lower jaw. The other piece, which has a single root and which may belong to

the same individual, was not described. Boonstra (1953a: 25) transferred the specimen to *Titanosuchus* but on page 28 regarded it as *incertae sedis*. Boonstra (1955a) resurrected *Scapanodon* on the basis of *S. septemfontis*. Haughton & Brink (1955: 46) retained SAM-769 in *Titanosuchus*. Boonstra (1969: 35) again regarded it as *Titanosuchus*, but considered the cranial features of this taxon to be indeterminate. He stated (1969: 35) that the humerus could not be distinguished from that of *Titanosuchus*, whilst the skull referred to this genus by Broom (1923) falls within the limits set by Boonstra for the genus *Jonkeria*.

Scapanodon septemfontis Boonstra, 1955

Holotype

SAM-5001

Material

Ilium, pubis, femur, humerus, ischium.

Locality

Sewefontein, Prince Albert.

Collected

Haughton, 1917.

Generic diagnosis

See Broom (1904) for diagnosis of *Scapanodon*.

Specific diagnosis

Humerus large, fairly long (480? mm); deltopectoral crest terminates far distally but still well away from ventral opening of entepicondylar foramen (after Boonstra 1955b: 271–272). Pelvis and femur as in generic diagnosis, as emended by Boonstra (1955b: 269–270). (See comments.)

References

Broom 1928: 431, figs 4, 5A.

Boonstra 1955b: 271–272, figs 60a, 61–62.

Comments

Broom (1904: 182) mentioned several other bones, including two humeri (SAM-772 and SAM-773) found in the same area as the type of *S. duplessisi* (SAM-769).

Boonstra (1955b) considered these specimens to belong to the same species as SAM-769 and based this new species (*S. septemfontis*) on the different humeral structure of SAM-5001. Boonstra (1955b) emended the generic diagnosis to include postcranial elements. Broom (1928) referred SAM-5001 to

Tapinocephalus atherstoni, while Boonstra (1955*b*) made it the type of a new species of *Scapanodon*, but earlier he (1953*a*) regarded *Scapanodon* (as known from Broom's *S. duplessisi*) as a junior synonym of *Titanosuchus*. Boonstra (1969), however, regarded *Scapanodon* as a junior synonym of *Titanosuchus ferox*.

Titanosuchus cloetei Broom, 1903

Holotype

SAM-731.

Material

Left anterior part of lower jaw.

Locality

Gamka River, Prince Albert.

Collected

Presented by Cloete.

Generic diagnosis

See Owen (1879) for diagnosis of *Titanosuchus*.

Specific diagnosis

Differentiated from *T. ferox* principally by dental measurements. Incisors in *T. cloetei* appreciably smaller, canine much smaller and rounder. In *T. cloetei* 4 molars occupy space of 40 mm, each root practically round and about 8,0 mm in diameter. Another difference is arrangement of anterior molars. In *T. ferox* the line of the molars is much on the inside of the large canine, but in *T. cloetei* a line drawn along inner sides of molars also forms a tangent to the canine. Front of jaw also very much squarer in smaller species owing to canine being relatively further forward. (After Broom 1903: 142–143.)

References

- Broom 1903: 142–143.
- Broom 1909*b*: 287.
- Haughton 1915*b*: 57.
- Broom 1929: 11, 25, fig. 25G.
- Broom 1932: 24, fig 6G.
- Boonstra 1953*a*: 27.
- Haughton & Brink 1955: 47.
- Boonstra 1962: 76–77, fig. 16.
- Boonstra 1969: 35.
- Kitching 1977: 36.

Comments

Broom (1929) transferred the specimen to *Jonkeria*. Boonstra (1953a) retained it as *Titanosuchus cloetei*. Boonstra (1969) noted that the specimen was determinable only to the family Titanosuchidae.

Titanosuchus dubius Haughton, 1915

Holotype

SAM-2759

Material

Right ramus of lower jaw.

Locality

Platfontein, Prince Albert.

Collected

Haughton, 1913.

Generic diagnosis

See Owen (1879) for diagnosis of *Titanosuchus*.

Specific diagnosis

Differs from *T. cloetei* in having a more massive symphysis, in being even squarer in the front of the jaw, and in the much larger canine and much smaller molars. Incisors similar in size but set much closer together. Canine narrower and longer, almost oblong in section with one side more than twice the length of the other. Molars smaller and circular in section. Line drawn along the inner side of molars just touches canine and is also tangential to inner surface of the fourth incisor. (After Haughton 1915b: 57.)

References

- Haughton 1915b: 57.
- Broom 1929: 33, fig. 25H.
- Broom 1932: 31, fig. 6H.
- Boonstra 1953a: 27.
- Haughton & Brink 1955: 46.
- Boonstra 1962: 77–78, fig. 17.

Comments

Haughton (1915b) considered *Titanosuchus* to be a therocephalian. Broom (1929) placed the species in a new genus *Dinocynodon*. Boonstra (1953a) retained it as *Titanosuchus dubius*. Boonstra (1969) stated that the poor preservation of the type made the taxon identifiable only to the family Titanosuchidae.

Family **Tapinocephalidae**

Subfamily Tapinocephalinae

Pelosuchus priscus Broom, 1905***Holotype***

SAM-918

Material

Right dentary, partial palate, femur, tibia, coracoid, scapula, rib fragments and seven vertebrae.

Locality

Bokfontein, Prince Albert.

Collected

Du Plessis and Cairncross.

Generic diagnosis

Jaws differ from those of therocephalians and dinocephalians in that the teeth cannot be distinguished as incisors, canines and molars. Remains or sockets of 8 teeth present, and anterior 5 larger than posterior 3; the last 3 do not seem to have distinct sockets, but are lodged in a groove. Vertebral bodies biconcave but not deeply concave. In some the transverse processes are very large and pass upwards and outwards as in some vertebrae of *Belodon*. In others the transverse processes pass outward and downward as in pelycosaurs. Coracoid large. (After Broom 1905: 335–336.)

Specific diagnosis

As for genus.

References

- Broom 1905: 335–336.
- Broom 1932: 46, fig. 3E-G.
- Boonstra 1955b: 186, 199, 216, fig. 7.
- Haughton & Brink 1955: 48.
- Boonstra 1956: 164–165.
- Von Huene 1956: 277.
- Orlov 1964: 256.
- Boonstra 1969: 42.

Comments

Broom (1905) provisionally placed *Pelosuchus* as a diaptosaurian, but in 1932 recognized it as a tapinocephalian. Boonstra (1969) proposed *Pelosuchus* as a junior synonym of *Keratocephalus*.

Subfamily Struthiocephalinae

Struthiocephalus whaitsi Haughton, 1915**Holotype**

SAM-2678

Material

Weathered skull without lower jaw.

Locality

Vivier Siding, Beaufort West.

Collected

Whaits.

Generic diagnosis

'Skull large; snout relatively long and slender; frontal and temporal regions not so much elevated above snout as in *Tapinocephalus*; eyes look forward and outward; heavy overhanging supraorbital crests; temporal fossae larger than orbits, elliptical in shape with shorter axis parallel to axis of skull; teeth weak, undifferentiated and few in number' (Haughton 1915a: 52).

Specific diagnosis

As for genus.

References

- Haughton 1915a: 52–54, pl. 10.
Gregory 1926: 240, fig. 29, table 5.
Broom 1932: 37, fig. 12C.
Boonstra 1951: 341.
Boonstra 1952a: figs 1–2.
Boonstra 1952b: 511.
Boonstra 1952d: 248.
Boonstra 1953b: 32, 46–47, 49–51.
Haughton & Brink 1955: 48–49.
Boonstra 1965b: 251.

Comments

Boonstra (1953b) provided emended generic and specific diagnoses of this taxon. Haughton & Brink's (1955) generic diagnosis differs from that given originally by Haughton (1915a). Boonstra (1969) recognized this species as the only valid species of *Struthiocephalus*.

Struthiocephalus akraalensis Boonstra, 1952**Holotype**

SAM-3719

Material

Good skull without lower jaw.

Locality

Abrahamskraal, Prince Albert.

Collected

Haughton.

Generic diagnosis

See Haughton (1915) for diagnosis of *Struthiocephalus*.

Specific diagnosis

Compared mainly to *S. whaitsi*, dorsal surface of parietal wider and not pinched in but frontal narrower and dorsally excavated; postfrontal and postorbital have larger dorsal exposure and squamosal forms a greater part of post-temporal arch, which is also of considerably stronger build. Much larger than any of the other described species. Pineal foramen lies further forward; median occipital ridge narrow and sharp and dorsal portion not broadened; postorbital bar forms at its junction with dorsal skull surface a strong ridge parallel to the mid-line and medial to this the surface of frontal and parietal hollowed out; the surface of the postorbital skull bones is coarse with deep rugae and crocodile-like pits. (After Boonstra 1952d: 247–248.)

References

- Boonstra 1952d: 247–248, figs 1–2.
- Boonstra 1952f: 238.
- Boonstra 1953b: 32, 50.
- Haughton & Brink 1955: 49.
- Boonstra 1969: 39.

Comments

With regard to the material, the museum catalogue states ‘skull and skeleton’, but there are no associated postcrania in the collection and nor are any referred to in any of Boonstra’s papers. Boonstra (1953b) provided an emended specific diagnosis and later (Boonstra 1969) proposed *S. akraalensis* as a junior synonym of *S. whaitsi*.

Struthiocephaloides cavifrons Boonstra, 1952

Holotype

SAM-5607

Material

Skull and scapula.

Locality

Lammerkraal, Prince Albert.

Collected

Haughton, 1916.

Generic diagnosis

Mormosaurid with skull similar to *Struthiocephalus*, but without nasofrontal boss and without interorbital postrostral step; moderately wide across the postorbitals; in dorsal view the postorbitals do not form lateral border of skull (after Boonstra 1952f: 237, 240).

Specific diagnosis

'Large; snout fairly high and strong; interorbital part of skull roof concave; distinct parietal boss; skull widest at level of postorbital arches; pineal foramen lies far back' (Boonstra 1952f: 241).

References

- Boonstra 1952f: 237–241, figs 1–3.
- Boonstra 1953b: 48.
- Boonstra 1955b: 236, fig. 29a–b.
- Haughton & Brink 1955: 49.
- Boonstra 1969: 39, 55.

Comments

Boonstra (1969) maintained that this was a valid taxon.

Struthiocephaloides duplessisi Boonstra, 1952

Holotype

SAM-11693

Material

Good skull.

Locality

Dikbome, Laingsburg.

Collected

Boonstra, 1946.

Generic diagnosis

See Boonstra (1952f) for diagnosis of *Struthiocephaloides*.

Specific diagnosis

‘[Skull] small; snout low and weak; interorbital skull roof convex; parietal boss not distinct; maximum width in region of temporal fossae; pineal foramen situated far anteriorly’ (Boonstra 1952f: 241).

References

- Boonstra 1952b: 509–511, figs 1–2.
Boonstra 1952f: 238, 241.
Boonstra 1954b: 32, 45.
Haughton & Brink 1955: 49.
Boonstra 1969: 39, 55.

Comments

Boonstra (1952b) made this specimen the type of *Struthiocephalus duplessisi* sp. nov., and later (1952f) transferred the species to his new genus *Struthiocephaloides*. Boonstra (1969) considered *Struthiocephaloides duplessisi* to be a valid taxon.

Struthionops intermedius Boonstra, 1952

Holotype

SAM-11947

Material

Distorted and somewhat weathered skull without lower jaw.

Locality

See comments.

Collected

Unknown.

Generic diagnosis

Skull fairly lightly built with slight pachyostosis; postorbital arch moderately strong, with no boss-like swelling of its upper part; posterodorsal circumorbital bones only slightly thickened with little overhanging of orbits; frontals excluded from orbital border; nasals and frontals only slightly thickened with very slight indication of a nasofrontal swelling; in sagittal plane the middle part of nasals forms concave dorsal surface and at nasofrontal junction surface moderately convex; pineal foramen penetrates small but prominent boss directed somewhat posteriorly; snout fairly long, wide and fairly high; temporal fossa medium-sized with dorsoventral diameter much greater than anteroposterior diameter; orbits large; interorbital width large; intertemporal width fairly large; intertemporal region laterally only slightly pinched in and without any indication of parietal crest; occiput inclined much anteriorly dorsoventrally; quadrates apparently only moderately shifted forward; probably

14–15 teeth in upper jaw; large frontals and prefrontals; parietals small; large pineal foramen situated near occipital border; postorbital apparently just meets squamosal, but parietal forms upper edge of temporal fossa (after Boonstra 1952c: 988–989).

Specific diagnosis

As for genus.

References

- Boonstra 1952c: 988–989, figs 1–2.
Boonstra 1952h: 246.
Boonstra 1953b: 48–50, 52–53.
Haughton & Brink 1955: 50.
Von Huene 1956: 277.
Piveteau 1961b: 277.
Boonstra 1963a: 178.
Boonstra 1963b: 202, 204, figs 3J, 4K.
Orlov 1964: 258.
Boonstra 1969: 41, fig. 10K.

Comments

While in the museum catalogue the locality is stated to be unknown, Boonstra (1952c) stated that it was probably recovered in the vicinity of Abrahamskraal, Prince Albert. Boonstra (1952c) originally placed this taxon in the Mormosauridae, a view which Orlov (1964) also supported. Boonstra (1953b) emended the diagnosis of this taxon. He (1969) considered this to be a valid taxon.

Struthiocephalellus parvus Boonstra, 1955

Holotype

SAM-5006

Material

Skull, scapula, humerus, ulna, pelvis, femur, proximal portion of tibia, vertebrae, and several small, unidentified fragments.

Locality

See comments.

Collected

Haughton, 1916–17.

Generic diagnosis

Skull about half size of *Struthiocephalus whaitsi*. Weak pachyostosis with postorbital bar relatively slender and post temporal opening roomy; occiput

fairly upright and quadrate not shifted very far anteriorly; snout moderately high; no frontonasal boss. Posterior tooth crowns spatulate in outline and labiolingually compressed. In one or two of the rear crowns there appears to have been a stronger central cusp with a weaker posterior and anterior cusp as in *Agnosaurus* and *Rhopalodon*.

Cervical vertebrae similar to *Moschops* and *Moschognathus* and to those of the synapsids generally. Proatlas stout. Atlas temnospondylus with paired neural arch lying on large atlantal intercentrum and odontoid-like pleurocentrum. Atlantal intercentrum large with facet for capitulum of atlantal rib. Axial neural arch halves fused to each other and to pleurocentrum to form holospondylous vertebra. Spine comb-shaped. Axial centrum laterally excavated below diapophysis with sharp ventral keel. Third intercentrum smaller than its predecessors. Third cervical vertebra deeply excavated below diapophysis so that ventrally it shows a sharp keel. Atlantal rib greatly flattened, small bone with weak shaft, greatly expanded leaf-like tuberculum and much weaker capitulum. (After Boonstra 1955a: 180–184.)

Specific diagnosis

As for genus.

References

- Boonstra 1955a: 180–184, figs 1–3.
Boonstra 1955b: 203, 225, 237–238, figs 27c, 29c, 30–33.
Von Huene 1956: 277.
Piveteau 1961b: 277.
Orlov 1964: 258.

Comments

The locality, according to the museum catalogue, is Wilgebosch-Drift, Beaufort West. Boonstra (1955a, 1955b) gave it as Abrahamskraal, Prince Albert.

Orlov (1964) placed this taxon into the Mormosauridae. Boonstra (1969) proposed to synonymize it with *Struthiocephalus* and recognized this specimen as a juvenile of *S. whaitsi*. Boonstra (1969) considered the material assigned to *S. parvus* to represent juvenile specimens of *Struthiocephalus whaitsi*. The legend to fig. 27c in Boonstra (1955b) erroneously reads *Struthiocephalus* instead of *Struthiocephalellus*.

Subfamily Riebeeckosaurinae

Riebeeckosaurus longirostris Boonstra, 1952

Holotype

SAM-3400

Material

Incomplete skull with part of lower jaw, vertebrae and several associated, unidentified bone fragments.

Locality

Near Vivier Siding, Beaufort West.

Collected

Whaits, 1915.

Generic diagnosis

'Tapinocephalid with large skull, long and quite narrow; snout long, narrow and quite high; cranial bones quite thickened; postorbital arch very massive; temporal fossa roomy with dorsoventral diameter much greater than anteroposterior diameter; intertemporal area very narrow and forms sagittal crest which curves downwards and backwards; parietal forms part of supratemporal edge; occiput very inclined; parietal very small; frontal large, does not form part of supraorbital border, but reaches supratemporal border; prefrontal forms supraorbital border; quadrate supported by anteriorly directed process of quadratojugal; teeth undifferentiated' (Boonstra 1952*h*: 248).

Specific diagnosis

As for genus.

References

- Boonstra 1952*h*: 246–249, figs 1–3.
- Haughton & Brink 1955: 53.
- Von Huene 1956: 277.
- Piveteau 1961*b*: 275.
- Boonstra 1963*a*: 178.
- Boonstra 1963*b*: 200, 205, figs 3E, 4F, 6F.
- Orlov 1964: 258.
- Boonstra 1969: 42, fig. 13.
- Boonstra 1971: 21, 33.

Comments

Boonstra (1963) placed this taxon in the subfamily Riebeeckosaurinae and in 1969 he placed that subfamily within the family Tapinocephalidae. Haughton & Brink (1955) proposed that the taxon be placed in the family Moschopidae, while Orlov (1964) considered it to represent the family Mormosauridae. Boonstra (1969) considered it to be a valid taxon.

Subfamily Moschopinae

Delphinognathus conocephalus Seeley, 1892**Holotype**

SAM-713

Material

Incomplete, weathered skull with part of lower jaw.

Locality

Doubtful—perhaps near Beaufort West, according to Seeley (1892).

Collected

?Bain, 1883.

Generic diagnosis

Broad, high and vertical occipital plate; large pineal foramen in middle of prominent boss (cone) with foramen at level of posterior border of orbit; orbits placed far back; quadratosquamosal region directed obliquely forward; lower jaw short and singularly deep posteriorly; occipital plate higher than wide; temporal fossa relatively small; prefrontal region concave; sub-ovate notch in inferior margin of posterior margin of posterior part of temporal arch (after Seeley 1892: 469–475).

Specific diagnosis

As for genus.

References

- Seeley 1892: 469–475, figs 1–2.
Broom 1910: 206, fig. 4.
Broom 1914: 135–136.
Gregory 1926: 228–230, 249, fig. 22a, tables II, III, IV.
Broom 1932: 44–45, fig. 9K.
Boonstra 1936: 93.
Haughton & Brink 1955: 51.
Von Huene 1956: 277.
Boonstra 1957: 15–17, 19–21, 27, 29, 33, 36–37, fig. 10.
Boonstra 1963a: 178.
Boonstra 1963b: 202, 205, figs 3F, 4G.
Orlov 1964: 258.
Boonstra 1969: 42, 55, fig. 11c.
Tatarinov 1976: 46.

Comments

Seeley's (1892) diagnosis of this taxon was emended by Broom (1932), Haughton & Brink (1955) and Boonstra (1957). Gregory (1926) placed the

taxon in the subfamily Moschopinae, while Boonstra (1936) and Orlov (1964) were prepared only to place it in the family Moschopidae. Boonstra (1963) placed it in the family Tapinocephalidae and in 1969 proposed that the specimen be regarded as a juvenile of *Moschops*. Tatarinov (1976) placed the taxon in the family Delphinognathidae.

Moschosaurus longiceps Haughton, 1915

Holotype

SAM-3015

Material

Good but weathered skull and six vertebrae.

Locality

La-de-da, Beaufort West.

Collected

Haughton, 1914.

Generic diagnosis

Skull long, low and narrow; parietal region slightly elevated but not tremendously thickened; nares rather far back; orbits in posterior half of skull and larger than temporal openings; quadrate in plane of middle of orbit; lower jaw massive; premaxillary teeth large with long anterior and smaller posterior cusps; postorbital bar comparatively weak; postorbital bone forms large part of upper border of temporal fossa; pineal foramen large and placed very far back (after Haughton 1915c: 78–81).

Specific diagnosis

As for genus.

References

- Haughton 1915c: 78–81, figs 8–9.
- Broom 1923: 663.
- Gregory 1926: 227, 241, fig. 21, table V.
- Broom 1932: 45, fig. 12D.
- Boonstra 1936: 93–95, 97.
- Boonstra 1952g: 243–244.
- Haughton & Brink 1955: 52–53.
- Von Huene 1956: 276, fig. 317.
- Boonstra 1955a: 183.
- Piveteau 1961b: 277.
- Boonstra 1963a: 178, 188.

Boonstra 1963*b*: 199–200, figs 2D, 3D, 4E.

Orlov 1964: 258, fig. 216.

Boonstra 1965*b*: 265, fig. 11.

Boonstra 1969: 39, fig. 10E.

Comments

Haughton (1915) considered this taxon to be titanosuchid, and Broom (1923) regarded the specimen as an immature titanosuchid. Gregory (1926) considered the taxon referable to the family Tapinocephalidae and erected the subfamily Moschosaurinae to accommodate it. Broom (1932) agreed that it represents a tapinocephalid as did Boonstra (1936), who erected Gregory's subfamily to familial rank, viz, Moschosauridae, and also emended the diagnosis of the taxon *Moschosaurus longiceps*. In 1963, however, Boonstra (1963*b*) changed the rank of the family Moschosauridae back to subfamilial status. Boonstra (1965*b*) proposed to synonymize the taxon with *Struthiocephalus*, a view that he maintained later (Boonstra 1969).

Agnosaurus pienaari Boonstra, 1952

Holotype

SAM-11832

Material

Weathered, incomplete skull.

Locality

Lammerkraal, Prince Albert.

Collected

Presented by Pienaar.

Generic diagnosis

'*Moschosaurus*-like Tapinocephalid [*sic*] with slight pachyostosis; large temporal fossa; snout quite long, high and narrow; quadrate shifted forward moderately; anterior teeth typical tapinocephaloid but posterior teeth with spatulate crowns and cylindrical roots' (Boonstra 1952*g*: 245).

Specific diagnosis

As for genus.

References

Boonstra 1952*g*: 242–245, fig. 1.

Boonstra 1953*b*: 52.

Haughton & Brink 1955: 52.

Boonstra 1955a: 182–183.

Von Huene 1956: 277.

Piveteau 1961b: 277.

Boonstra 1963a: 178.

Orlov 1964: 258.

Boonstra 1969: 42.

Comments

Orlov (1964) placed this taxon in the family Moschosauridae. Boonstra (1969) regarded *A. pienaari* as a junior synonym of *Moschops*.

Avenantia kruisvleiensis Boonstra, 1952

Holotype

SAM-9166

Material

Nearly complete skull, proximal part of femur, two vertebrae, ?fibula and two unidentified fragments. See comments.

Locality

Kruisvlei, Beaufort West.

Collected

Boonstra, 1929.

Generic diagnosis

‘Moschopid-like Tapinocephalid [sic], but exoccipital forms part of condyle, narrow intertemporal region, low parietal crest, postorbital meets squamosal in temporal fossa, pineal foramen surrounded by a distinct ridge’ (Boonstra 1952i: 225).

Specific diagnosis

As for genus.

References

Boonstra 1952h: 248.

Boonstra 1952i: 250–255, figs 1–3.

Haughton & Brink 1955: 50.

Boonstra 1955b: 258.

Von Huene 1956: 276.

Boonstra 1957: 16–22, 24–28, 33, 35–37, fig. 11.

Boonstra 1963a: 178.

Boonstra 1963b: 202, 205, figs. 3G, 4H.

Orlov 1964: 258.

Boonstra 1969: 42, 55.

Boonstra 1971: 21, 33.

Comments

There is some doubt regarding the postcranial material labelled SAM-9166. Specimens SAM-9166 and SAM-9167 are from the same locality, and Boonstra (1952*i*) noted that SAM-9166 is one of a 'wagon-load of specimens found partially weathered out in a small area'. The museum catalogue entry for SAM-9166 notes only 'skull'; the entry for SAM-9167 notes 'ilium, femur, fibula, vertebrae'. Boonstra (1955*b*) mistakenly referred to SAM-9167 as the type of *Avenantia kruisvleiensis*, and recorded it as having scapula, ilium, femur, and skull. The museum catalogue entry for SAM-9167, however, does not refer to a skull. It appears that the postcranial material labelled SAM-9166 may belong instead to SAM-9167.

Boonstra (1957) provided an emended diagnosis for this taxon. Orlov (1964) referred it to the family Moschopidae and Boonstra (1969) referred it to the subfamily Moschopinae as a valid taxon.

Boonstra (1952*h*) referred to *Avenantia kruisvleiensis* in an article which preceded the paper (Boonstra 1952*i*) in which the type description of the taxon was given. Accordingly, Boonstra's (1952*h*) use of the name *Avenantia kruisvleiensis* made it a *nomen nudum*. However, *Avenantia kruisvleiensis* was made available in his second paper (Boonstra 1952*i*).

Moschops koupensis Boonstra, 1957

Holotype

SAM-11582

Material

Good skull with part of lower jaw.

Locality

Die Krans, Prince Albert.

Collected

Boonstra and Bothma, 1940.

Generic diagnosis

See Broom (1911) for diagnosis of *Moschops*.

Specific diagnosis

'[Skull] very wide across parietals with interorbital width 70 per cent of intertemporal width. Snout relatively narrow. Occipital surface greatly reduced by overgrowth from above and from the sides. Transverse pterygoidal rami are strong.' (Boonstra 1957: 32-33.)

References

- Boonstra 1957: 18–19, 21–26, 32–33, figs 5–9.
Boonstra 1969: 42.

Comments

Boonstra (1969) considered this specimen to represent a valid species of *Moschops*.

Family **Styracocephalidae**

Styracocephalus platyrhynchus Haughton, 1929

Holotype

SAM-8936

Material

Incomplete, crushed and badly weathered skull and part of lower jaw.

Locality

Boesmansrivier, Beaufort West.

Collected

Boonstra, 1928.

Generic diagnosis

Most striking features are large backwardly projecting tabular horns, massiveness of bones in postorbital region, small temporal opening, swollen cheek-like quadratojugal, and shallowness of snout which is also fairly long and narrow. Pineal foramen small and situated in middle of low, broad swelling in middle of parietal surface. Teeth present on pterygoids and palatines. (After Haughton 1929: 55–57.)

Specific diagnosis

As for genus.

References

- Haughton 1929: 55–60, figs 3–5.
Broom 1932: 139, fig. 47A.
Boonstra 1934: 465, 467–470.
Romer 1945: 601.
Haughton & Brink 1955: 54.
Von Huene 1956: 287–288.
Heyler 1961: 127.
Boonstra 1963a: 176–178, 188, figs 2L, 3J, 4H, 12.

- Boonstra 1963b: 196, 199, 206, figs 1, 2, 3C, 4D, 5G, 6G.
 Orlov 1964: 267.
 Romer 1966: 372.
 Boonstra 1969: 44, fig. 14.
 Boonstra 1971: 18, 22, 24–26, 33–34, 40, 42, fig. 3.
 Boonstra 1972: 316, 321, 325–326, fig. 2.
 Tatarinov 1974: 51–52.
 Kitching 1977: 33.

Comments

Haughton (1929) referred this taxon to a new suborder, Styraçocephalia. Broom (1932) placed it into another suborder, Burnetiamorpha, and considered that the specimen's affinities were with the Gorgonopsia rather than with the Dinocephalia. Boonstra (1934) regarded the specimen as a dinocephalian and maintained it in Haughton's Styraçocephalia. Romer (1945) followed Broom, however, placing the taxon in the Gorgonopsia and in the family Burnetiidae (=Burnetiamorpha of Broom). Haughton & Brink (1955) followed Boonstra (1934) and placed it in the Dinocephalia, using Haughton's subordinal classification of Styraçocephalia. Heyler (1961) followed Romer (1945), however, and placed it in the gorgonopsian family Burnetiidae. Von Huene (1956: 287) considered this taxon to belong to the Dinocephalia, but placed it into the 'Familienkreis u. Familie Burnetiamorpha'. Boonstra (1963a) still considered it to be a dinocephalian and proposed the new family rank, Styraçocephalidae for its placement. Orlov (1964) regarded it as belonging to the Burnetidae [*sic*] of the Gorgonopsoidea, and Romer (1966) re-affirmed his earlier (1945) conviction of its taxonomic placement. Boonstra (1969, 1971) proposed to maintain it in the family Styraçocephalidae, which he regarded in 1972 as belonging to the Titanosuchia. Tatarinov (1974) considered that the taxon should be placed in the Burnetiidae of the order 'Gorgonopia', whilst Kitching (1977) maintained that *Styraçocephalus* is a tapinocephalid and should be placed in the subfamily Tapinocephalinae.

ACKNOWLEDGEMENTS

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Family **Nuculanidae**

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch.*, Paris 88: 100-140.
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(continued inside back cover)

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CRETACEOUS FAUNAS FROM
ZULULAND AND NATAL, SOUTH AFRICA
ADDITIONAL OBSERVATIONS ON THE
AMMONITE SUBFAMILY TEXANITINAE
COLLIGNON, 1948

By

WILLIAM JAMES KENNEDY
HERBERT CHRISTIAN KLINGER
&
HERBERT SUMMESBERGER

Cape Town Kaapstad

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CRETACEOUS FAUNAS FROM ZULULAND AND NATAL,
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ADDITIONAL OBSERVATIONS ON THE
AMMONITE SUBFAMILY TEXANITINAE COLLIGNON, 1948

By

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Naturhistorisches Museum, Vienna

(With 27 figures)

[MS accepted 11 June 1981]

ABSTRACT

Data supplementary to the monograph on the ammonite subfamily Texanitinae Collignon, 1948, by Klinger & Kennedy are given. These include a redescription and illustration of the type material and other Austrian and French specimens of *Ammonites serratomarginatus* Redtenbacher, 1873, and *Ammonites quinquenodosus* Redtenbacher, 1873. New material permits a study of the intraspecific variation in *Reginaites zulu* Klinger & Kennedy, 1980, and the homoeomorphy between it and *Plesiotexanites* (P.) *stangeri* (Baily, 1855). Two micromorph specimens of *Submortoniceras woodsi* (Spath, 1921) are homoeomorphic with *Protexanites* (P.) *bontanti shimizui* Matsumoto, 1970, exhibit traces of colour banding, and raise the possibility of sexual dimorphism in the subfamily Texanitinae.

CONTENTS

	PAGE
Introduction	116
Location of specimens	116
Dimensions of specimens	116
Suture terminology	116
Annotation of ornament	116
Systematic palaeontology	117
On <i>Ammonites serratomarginatus</i> Redtenbacher, 1873 and <i>Ammonites quinquenodosus</i> Red- tenbacher, 1873	117
Intraspecific variation in <i>Reginaites zulu</i> Klinger & Kennedy, 1980, and homoeomorphy with <i>Plesiotexanites</i> (P.) <i>stangeri</i> (Baily, 1855). . .	137
Colour banding in micromorphs of <i>Submortoni- ceras woodsi</i> (Spath, 1921) and their homoeo- morphy with <i>Protexanites</i> (P.) <i>bontanti shimi- zui</i> Matsumoto, 1970	149
Acknowledgements	153
References	153

INTRODUCTION

Subsequent to Klinger & Kennedy's (1980a) monographical description of the South African representatives of the ammonite subfamily Texanitinae Collignon, 1948, additional data from South Africa and Europe became available which are supplementary to the overall account already published. Part of these were published separately (Klinger & Kennedy 1980b). Although these data deal with different and remotely related aspects of the subfamily Texanitinae, economic measures deemed it advisable to publish these under one cover with appropriate subtitles. Authorship according to seniority is given below each subtitle. Authorship for the whole publication is in alphabetical order.

LOCATION OF SPECIMENS

The following abbreviations are used to indicate the repositories of the material studied:

FSR	Faculté des Sciences, Rennes, France
GBA	Geologische Bundesanstalt, Vienna, Austria
LL	Oberösterreichisches Landesmuseum, Linz, Austria
NHMW	Naturhistorisches Museum, Vienna, Austria
NS	Haus der Natur, Salzburg, Austria
SAM	South African Museum, Cape Town, South Africa
SAS	Geological Survey of South Africa, Pretoria

DIMENSIONS OF SPECIMENS

Dimensions of specimens are given in millimetres; abbreviations are as follows:

D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter, R = ribs per whorl, U : E tbs = ratio of umbilical to external tubercles.

Figures in parentheses are dimensions as a percentage of total diameter.

SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916; see Kullmann & Wiedmann 1970 for a recent review) is followed in the present work:

I = internal lobe, U = umbilical lobe, L = lateral lobe, E = external lobe.

ANNOTATION OF ORNAMENT

This follows the scheme presented in Klinger & Kennedy (1980a: 3-4); tubercles are numbered in ontogenetic sequence from the umbilical wall to the venter; e.g. umbilical tubercle is (1), lateral tubercle (2), submarginal (3), marginal (4), and external (5).

SYSTEMATIC PALAEONTOLOGY

ON *Ammonites serratmarginatus* REDTENBACHER, 1873, AND
Ammonites quinquenodosus REDTENBACHER, 1873.

(By W. J. Kennedy, H. Summesberger & H. C. Klinger)

Revision of the texanitid faunas of the South African Upper Cretaceous (Klinger & Kennedy 1980a) raised a number of questions, amongst others the effect of differential preservation and geographic morphological variation in *Ammonites serratmarginatus* and *Ammonites quinquenodosus*, two species from the Gosau Beds of the Austrian Alps described almost a century ago by Anton Redtenbacher (1873). It has now proved possible to locate some of the type material of these two species, as well as a series of other Austrian specimens.

Paratexanites serratmarginatus (Redtenbacher, 1873)

Figs 1–7

Ammonites serrato-marginatus Redtenbacher, 1873: 110, pl. 25 (fig. 2a–d)

Mortoniceras serrato-marginatum (Redtenbacher): De Grossouvre, 1894: 69, pl. 16 (fig. 1a–b).
 Pervinquière, 1907: 242. Diener, 1925: 148.

Bevahites (*Parabevahites*) *serrato-marginatus* (Redtenbacher): Collignon, 1948: 83(38).

Non Parabevahites serrato-marginatus (Redtenbacher): Collignon, 1966: 76, pl. 486 (figs 1962–1963).

Non Parabevahites cf. *serrato-marginatus* (Redtenbacher): Collignon, 1966: 80, pl. 488 (figs 1967–1969).

Paratexanites (*Parabevahites*) *serratmarginatus* (Redtenbacher): Matsumoto, 1970: 260, pl. 36 (figs 1–3), text-fig. 16. Matsumoto & Hirano, 1976: 337, text-fig. 3.

Paratexanites (*Parabevahites*) *serratmarginatus grossouvrei* Matsumoto, 1970: 263.

Paratexanites (*Parabevahites*) cf. *serratmarginatus* (Redtenbacher): Kennedy & Kollmann, 1977: 414, pl. 1 (fig. 1a–c).

Types

Redtenbacher based this species on seven syntypes, all of which have been traced. NS 6381, the original of Redtenbacher 1873, pl. 25 (fig. 2a–b) is the lectotype; paralectotypes are NS 6376, 6379, 6387, 6384, 6385, 6387. Four further specimens may also be part of the type series: NS 18427–18428 (part and counterpart), NS 18435, LL 26590, and 26598, all from the Coniacian Gosau Beds of Glanegg, Austria.

Other specimens studied

NHMW 1978/2029/3 from the Coniacian Beds of Glanriedel, Austria, FSR 'A', Seunes Collection, FSR 2834 and 2835, all from the Coniacian Craie de Villedieu of La Ribochère, commune de Couture, Loir-et-Cher, France.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>	<i>R</i>
NS 6381	45,2	16,2(38)	14,0(33)	1,15	15,0(35)	38–39?
FSR 2834	58,5	—	—	—	23,0(39)	21
FSR 'A'	72,3	—	24,5(34)	—	29,8(41)	27

Description

The lectotype (Figs 1A–C, 2I, 3B) is a small, distorted, composite internal mould just over 42 mm in diameter.

Coiling is evolute, only 25 per cent of the previous whorl being covered. The umbilicus is of moderate width (c. 35 per cent of diameter?) with a low, rounded wall. The whorl section is slightly depressed (due to post-mortem crushing), with greatest breadth below mid-flank.

Ornament consists of numerous slightly flexed, crowded prorsiradiate ribs, approximately 40 per whorl. Most arise singly from bullae (1) at the umbilical shoulder (although a few arise in pairs or are intercalated), and bear small, weakly clavate submarginal (3) and closely spaced, stronger marginal (4) tubercles. There are stronger external (5) clavi on either side of a narrow keel flanked by shallow sulci.

The earliest ontogenetic stages are seen in NS 6384 (Fig. 2G–H) and LL 26598 (Fig. 2A–B). Here, ribbing is again crowded and flexuous, with the distinctive close spacing of tubercles 3 + 4 visible even at a whorl height of only 5,5 mm. The former specimen has a compressed whorl section, presumably due to crushing, but reveals a better preserved keel than the lectotype, and this shows unmistakable undulations corresponding to the external (5) clavi. This is also seen, but is less prominent, in LL 26598, which differs from the lectotype in having the submarginal (3) tubercle longer and more prominent than the marginal (4) (Fig. 2A–B). Of the specimens corresponding in size to the lectotype, NS 18428 (NS 18427 is the counterpart) (Figs 1D, 3C) is coarser ribbed, with stronger bullae (1) and a greater forward projection to the ventrolateral ribbing. This is also seen in NS 6379 (Fig. 1I). In contrast, NS 6382 (Figs 1K, 3D), although crushed, is as densely ribbed as the lectotype.

Of the larger specimens, NS 6387, is the original of Redtenbacher 1873, pl. 25 (fig. 2C–D). It has a maximum whorl height of 20,5 mm, and appears to be sparser ribbed than the lectotype, as do all the larger specimens, suggesting outer whorls were consistently more distantly ribbed than the nuclei (Figs 1F–G, 3A). The ribs are flexuous with the submarginal (3) and marginal (4) tubercles close together, both clavate, and the former weaker than the latter (Figs 1G, 3A). The keel is well preserved, and feebly undulose. NS 6376 is identical, as far as it is preserved (Fig. 1E). In contrast, NS 18453 (Fig. 1H) shows the submarginal (3) and marginal (4) tubercles to be relatively stronger in relation to the ribs, with the submarginal (3) far more prominent, although shorter than the marginal (4). The largest and most ontogenetically advanced fragment, LL 26590 (Fig. 2C–D) shows a distinctly undulose keel and submarginal (3) and marginal (4) tubercles grouped on a swelling on the ventrolateral shoulder, with the external (5) clavi seemingly linked by weak ridges, which are much accentuated by crushing (Fig. 2D).

None of these specimens shows the sutures.

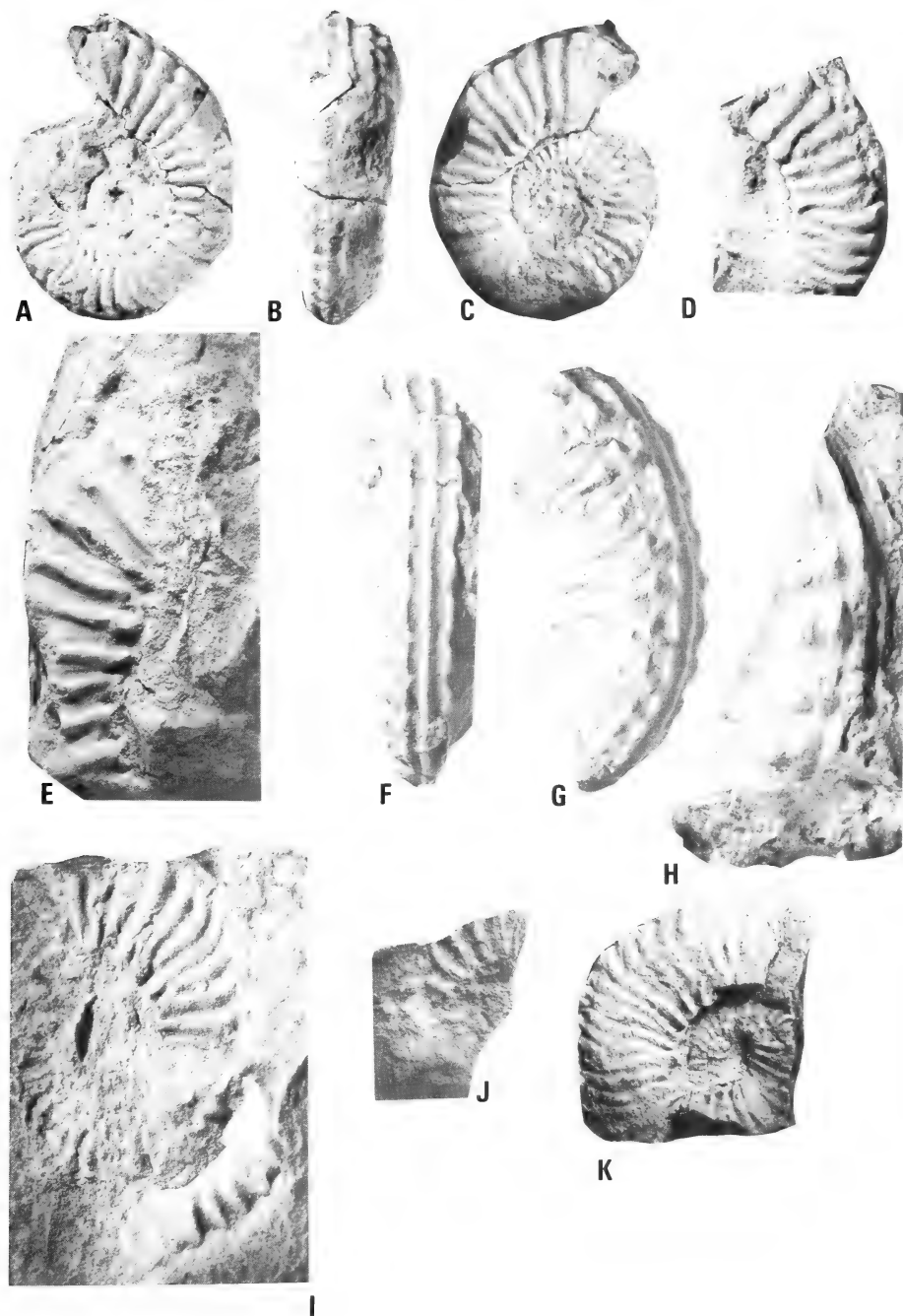


Fig. 1. *Paratexanites serratomarginatus* (Redtenbacher). A–C. The lectotype, NS 6381, the original of Redtenbacher (1873), pl. 25 (fig 2a–b). D. Paralectotype, NS 18428. E. Paralectotype, NS 6376. F–G. Paralectotype, NS 6378, the original of Redtenbacher (1873), pl. 25 (fig. 2c–d). H. Paralectotype, NS 18453. I. Paralectotype, NS 6379. J. Paralectotype, NS 6385. K. Paralectotype, NS 6382. All specimens are from the Coniacian Gosau Beds of Glanegg, Austria. $\times 1$.

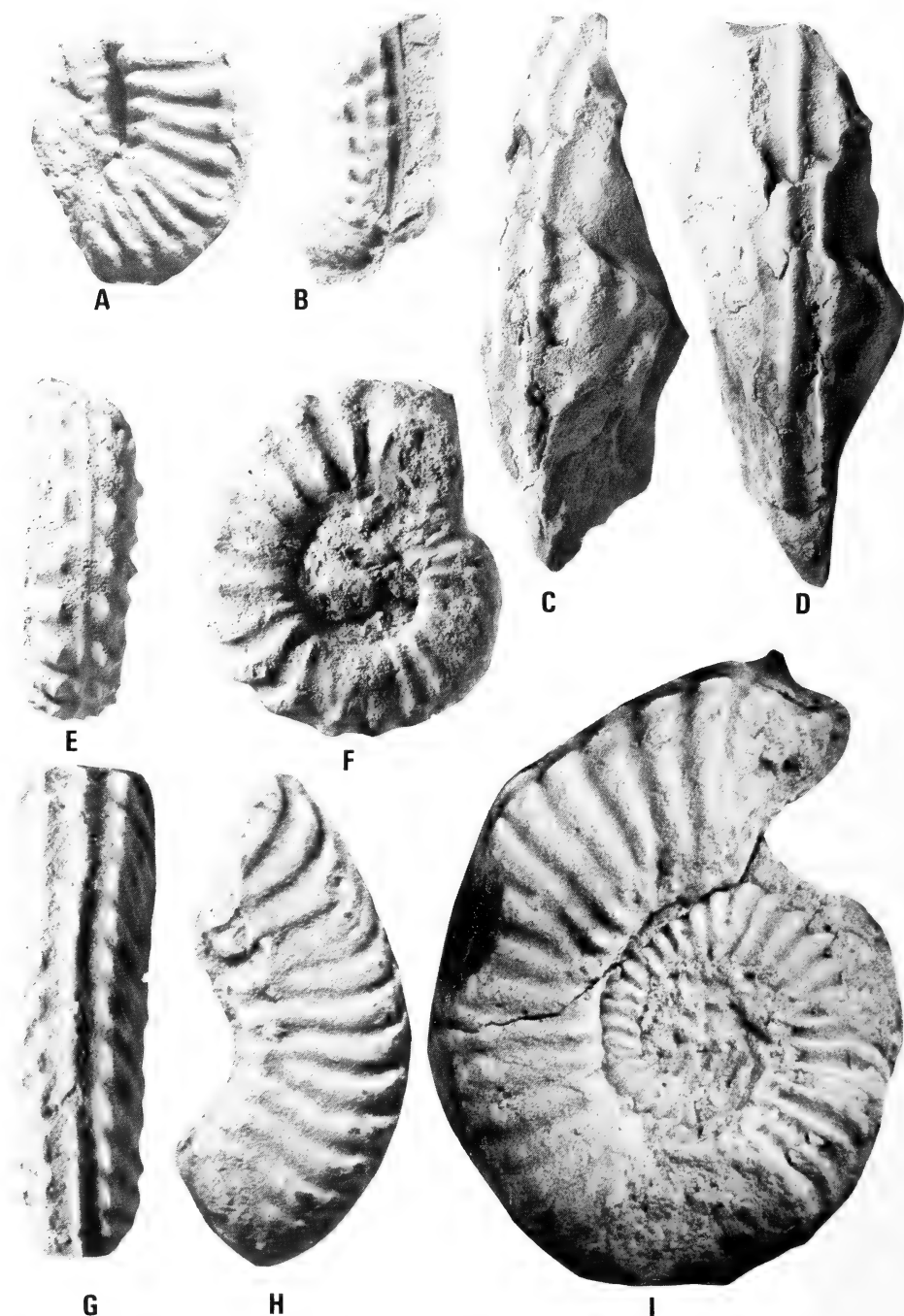


Fig. 2. *Paratexanites serratomarginatus* (Redtenbacher). A-B. Paralectotype, LL 26598. C-D. Paralectotype, LL 26590. E-F. FSR 2835. G-H. Paralectotype, NS 6384. I. Lectotype, NS 6381. A-D, G-I are from the Coniacian Gosau Beds of Glanegg, Austria; E-F is from the Coniacian Craie de Villedieu of La Ribochère, Loir-et-Cher, France. A-B, I $\times 2$; C-D, E-F $\times 1$; G-H $\times 4$.

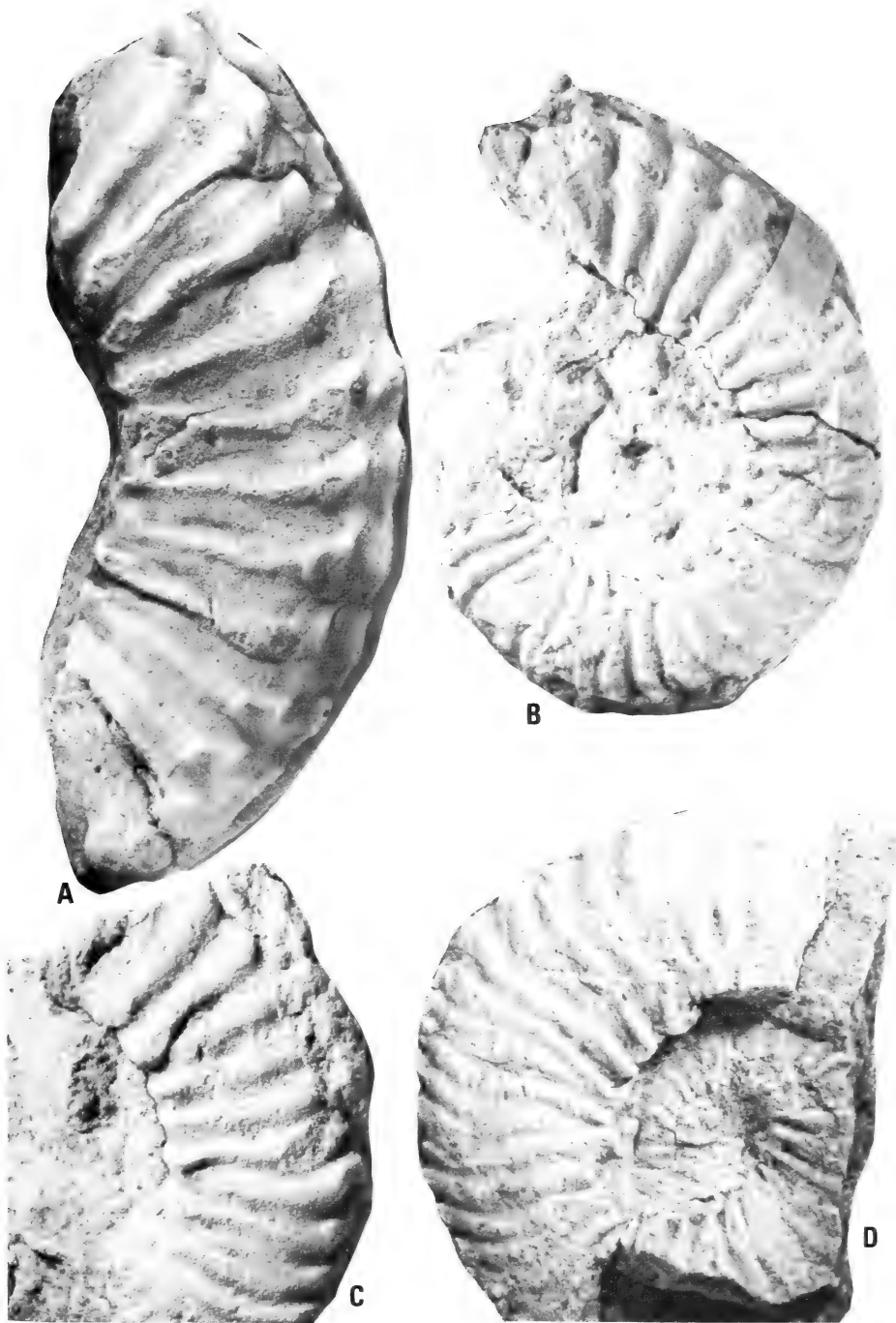


Fig. 3. *Paratexanites serratomarginatus* (Redtenbacher). A. Paralectotype, NS 6387. B. Lectotype, NS 6381. C. Paralectotype, NS 18428. D. Paralectotype, NS 6382. All specimens are from the Coniacian Gosau Beds of Glanegg, Austria. $\times 2$.

Discussion

The above description, based entirely on material from Glanegg, shows this species to be variable in both density and strength of ornament. A small, compressed specimen from Glanriedel, Austria, NHMW 1978/2029/3 (Fig. 4), is comparable to material from Glanegg. De Grossouvre (1894: 69, pl. 16 (fig. 1a-b) refigured herein as Fig. 7A-B) described a much larger specimen from the Craie de Villedieu of La Ribochère, Couture, Loir-et-Cher, France, which Matsumoto (1970: 263) has designated holotype of the subspecies *P. serratomarginatus grossouvrei*. Matsumoto (1970: 262) differentiated it from the Austrian form because of the 'stronger and more rounded inner ventrolateral

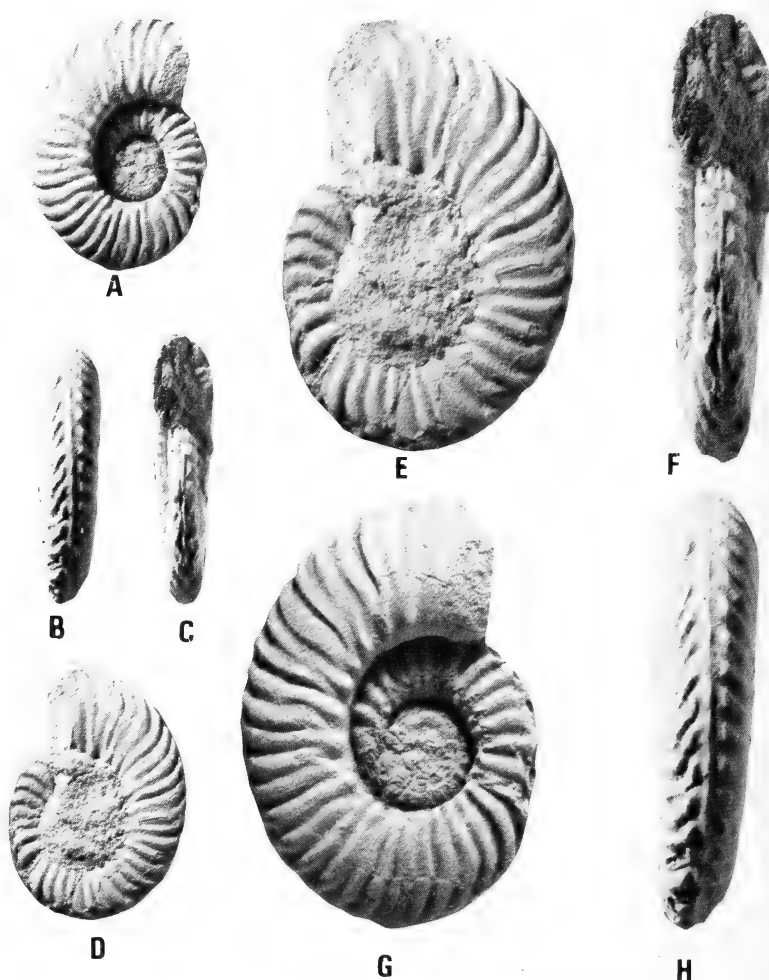


Fig. 4. *Paratexanites serratomarginatus* (Redtenbacher) NHMW 1978/2029/3 from the Coniacian Gosau Beds of Glanriedel, Austria. A-D $\times 1$; E-H $\times 2$.

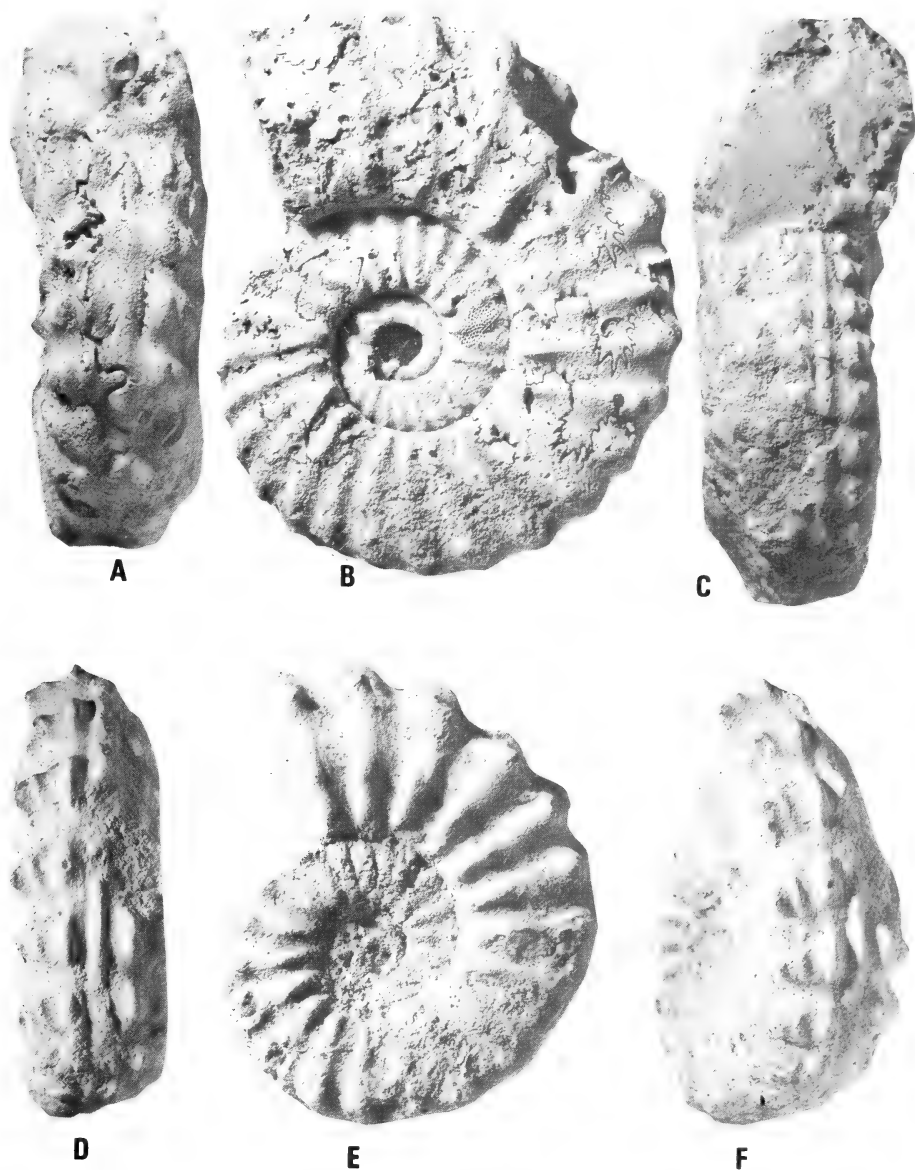


Fig. 5. *Paratexanites serratomarginatus* (Redtenbacher). A-C. FSR 'A', Seunes Collection. D-F. FSR 2834. Both specimens from the Coniacian Craie de Villedieu of La Ribochère, Loir-et-Cher, France. $\times 1$.

tubercles which are approximated to the outer ones, forming double ventrolateral major protruberances . . . the ventral keel shows weak undulations which correspond in number to the radial ribs, but in the Alpine species the keel is continuous and not undulated'. As the description of the Austrian material shows, the criterion of undulose v. continuous keel is not valid. Equally our largest and ontogenetically most advanced specimen (Fig. 2C-D) shows the double protruberance of the holotype of *P. serratomarginatus grossouvrei*, and there is such variation in the relative development of submarginal (3) and marginal (4) tubercles in the Austrian type series that this scarcely seems a criterion for separation.

The authors figure, however, three smaller French specimens from the Coniacian part of the Craie de Villedieu de La Ribochère (Figs 2E-F, 5A-F, 6) that show a greater range of variation and more advanced ontogenetic develop-

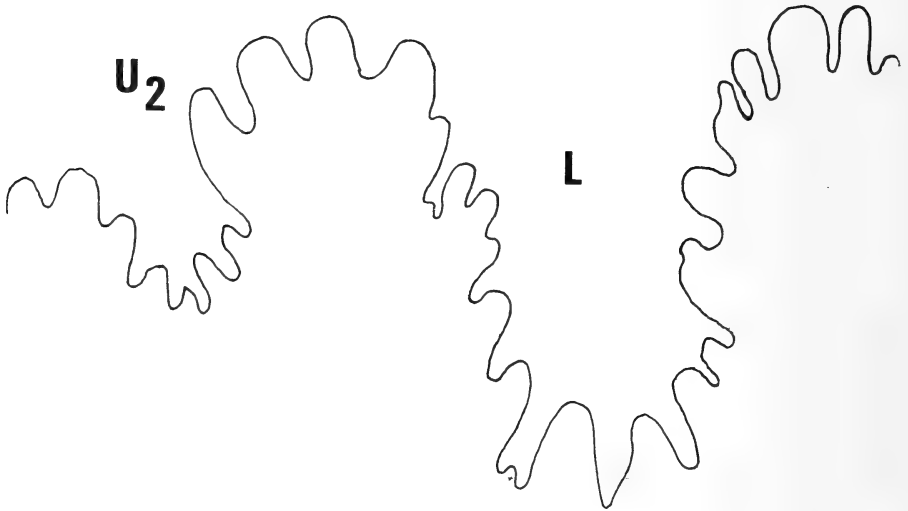


Fig. 6. *Paratexanites serratomarginatus* (Redtenbacher). External suture of FSR 'A', Seunes Collection. $\times 6$.

ment than is seen in the Austrian specimens. All are sparser ribbed than the lectotype, some with only half as many ribs at a somewhat greater diameter, although there is overlap in rib density with other types. FSR 'A' (Fig. 5A-C) is very close indeed to the Austrian type material, but FSR 2835 (Fig. 2E-F) is a curious, slowly expanding form with fewer ribs, which are more flexuous and have stronger bullae, with the marginal (4) tubercle very small indeed (Fig. 2E). FSR 2834 (Fig. 5D-F) shows similar features, especially the prominence of the submarginal (3) tubercle, while the marginal (4) tubercle is almost indistinguishable at the beginning of the last whorl, although strengthening towards the aperture. Given this variation and the overlap between the Austrian and

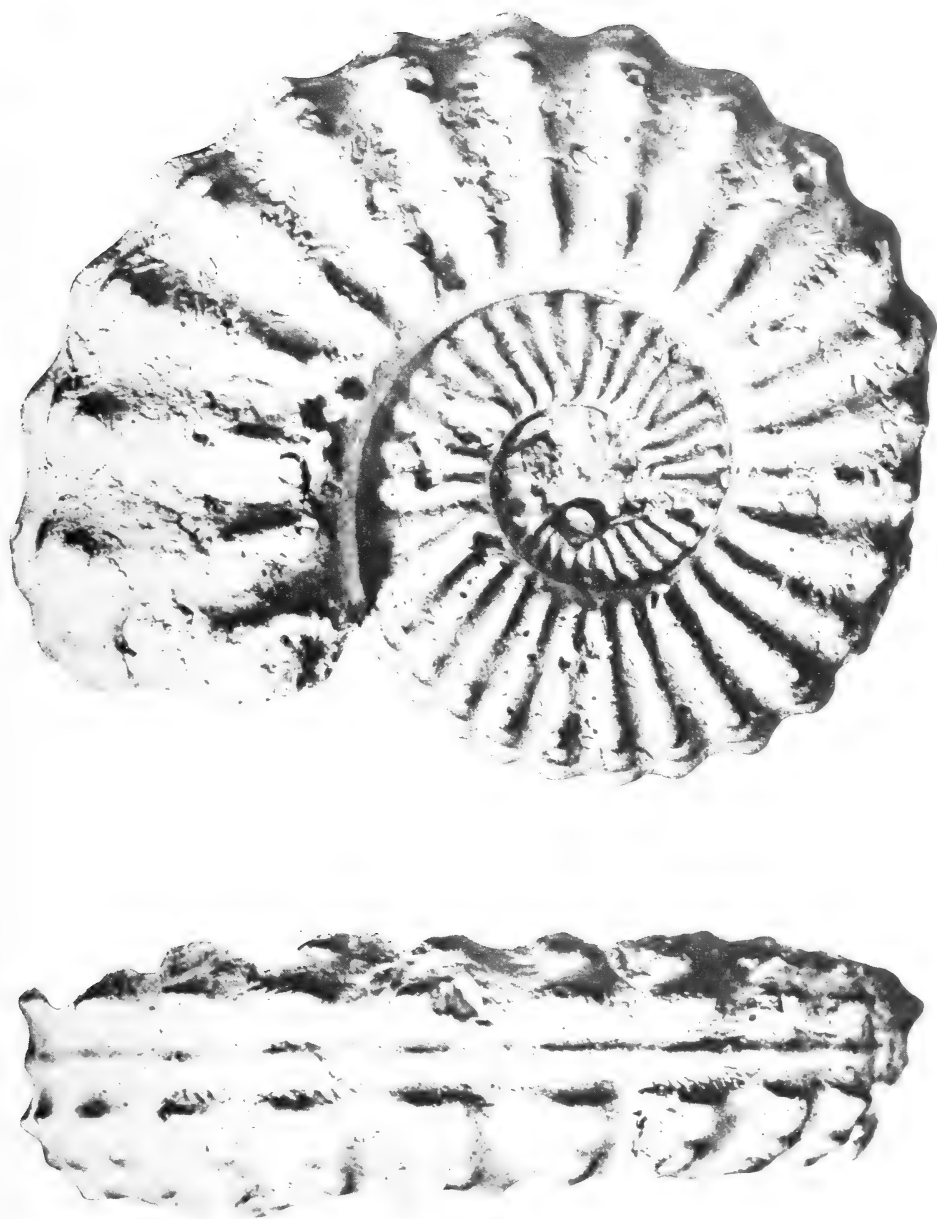


Fig. 7. The holotype of *Paratexanites serratomarginatus* (Redtenbacher) *grossouvrei* Matsumoto, from the Coniacian Craie de Villedieu of La Ribochère, Loir-et-Cher, France. Copy of De Grossouvre 1894, pl. 16 (fig. la-b). Reduced $\times 0.9$.

French specimens, we doubt that they merit subspecific separation, although acknowledging differences in variation range.

Specimens described from Japan by Matsumoto (1970: 260, pl. 36 (figs 1–3), text-fig. 16) fall into *P. serratomarginatus* as here interpreted. Collignon's (1966) specimens have a lateral tubercle and should be referred to *Plesiotexanites*, while we would continue to refer to the Zululand material (Klinger & Kennedy 1980a: 59, figs 45–47A) as *Paratexanites* sp. aff. *P. serratomarginatus*.

When compared to other 'Parabevahites', *Paratexanites emscheris* (Schlüter, 1876: 155, pl. 42 (figs 8–10)) has coarser, straighter ribs and umbilical bullae low on the flank rather than perched on the umbilical shoulder, and there are other differences as noticed by Matsumoto (1970: 262). *Paratexanites sellardsi* Young (1963: 79, pl. 32 (fig. 7), pl. 36 (figs. 3–5), pl. 37 (fig. 1), pl. 39 (fig. 4), pl. 49 (fig. 3), text-fig. 17) is also more coarsely ribbed and robustly tuberculate.

Occurrence

The type specimens are from Glanegg, Austria. Other ammonites from this locality (Brinkmann 1935: 2; Kennedy & Summesberger, in preparation) include *Gaudryceras glaneggense* (Redtenbacher), *Otoscaphtes arnaudi* (De Grossouvre), 'Ammonites' *aberlei* Redtenbacher, *Gauthiericeras margae* (Schlüter), and *Protexanites* sp. juv. These suggest a stratigraphic level way above the base of the Coniacian stage. The species is also recorded from France, Tunisia and Zululand and, where reliably dated, is also of Coniacian age.

Texanites quinquenodosus (Redtenbacher, 1873)

Figs 8–16

- Ammonites texanus* von Hauer (*non* Roemer, 1852) 1858: 10, pl. 2 (figs 4–6).
Ammonites quinquenodosus Redtenbacher, 1873: 108, pl. 24 (fig. 3a–b).
Mortoniceras texanus Schlüter sp.: Zurcher, 1905: 686.
Mortoniceras quinquenodosum (Redtenbacher): Yabe & Shimizu, 1923: 30 (*partim*).
Mortoniceras quinquenodosum [*lapsus*] (Redtenbacher): Diener, 1925: 147 (*partim*).
 ?*Texanites quinquenodosus* var. *evoluta* Haas, 1942: 18, text-fig. 12.
Texanites quinquenodosus (Redtenbacher): Collignon, 1948: 69, text-fig. 2; ?1966: 128, pl. 510 (fig. 2021). Thomel, 1969: 12, pl. G (figs 1–2). Klinger & Kennedy 1980a: 135, figs 102–3.
Texanites (*Texanites*) *quinquenodosus* (Redtenbacher): Matsumoto, 1970: 272. Wiedmann, 1979: 48, pl. 7 (figs C–D).
Texanites aff. *quinquenodosus* (Redtenbacher): Fabre-Taxy, 1963: 17, pl. 1 (fig. 14).
Texanites (*Texanites*) sp. aff. *T. (T.) quinquenodosus* (Redtenbacher): Matsumoto, 1970: 273, pl. 42 (fig. 3a–b), pl. 46 (figs 1–3).

Type

The lectotype is GBA 1873/01/13, the original of Redtenbacher 1873, pl. 24 (fig. 3a–b), from the Santonian Gosau Beds of St Wolfgang, Ischl, Austria.

Other specimens studied

In addition to the lectotype, the following specimens were available: LL 41/1938, a paralectotype, from the Schneiderwirtsbrücke, Ischl; LL 32 from Gosau; GBA 1873/01/13 (SV 2569), a paralectotype from Gosau; NHMW 1935.III.39, from Grabenbach, Gosau; NHMW 1926.II.2469, from the Nefgraben, Russbach, Gosau; NHMW 1935.III.40, from Gosau; GBA, an unregistered fragment from Gosau, and a possible paralectotype; NHMW 1935.III.41, from Gosau; and Böhm Collection from the Nefgraben, Gosau. All specimens are of Santonian age.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>	<i>R</i>
NHMW 1935.III.40	118,5	32(27)	40(34)	0,8	51(43)	27

Description

The lectotype (Fig. 8) is a flattened and distorted internal mould with almost a whorl of body chamber preserved, and a maximum diameter of almost 160 mm. Coiling is very evolute, the inner whorls being exposed to the outer ventrolateral (4) tubercle, which is housed in a small notch in the umbilical wall of the succeeding whorl. In the best preserved specimen, NHMW 1935.III.40 (Figs 12–13, 14A), the broad, shallow umbilicus comprises 43 per cent of the diameter. Uncrushed specimens show the intercostal whorl section to have been high oval with convergent flanks and a breadth to height ratio of 0,75. The costal section is also compressed, with the maximum width at the lateral (2) tubercle, and a breadth to height ratio of 0,87.

Ornament consists of numerous (27–32) straight, simple, recti- to slightly prorsiradiate ribs. These arise at the umbilical seam, and bear a pointed umbilical (1) bulla directed into the umbilicus. There are a larger, feebly clavate lateral (2) tubercle, a larger, clavate submarginal (3) tubercle and a strong clavate marginal (4) tubercle, and a long external (5) tubercle, which tends to link with its neighbours into an undulose keel. There is a strong, faintly undulose siphonal keel flanked by distinct grooves (Fig. 14A–B).

On adult body chambers (e.g. LL 41/1938 (Figs 15–16)), the tubercles decline and the ribs crowd towards the aperture.

The suture line is quite simple (Fig. 11) with moderately incised elements.

Discussion

Specimens available vary somewhat in strength and number of ribs while, when shell is preserved, the tubercles are also much sharper than on moulds during early growth (Figs 9–10), and there are strong transverse growth striae in adults (Figs 15–16).

Matsumoto (1970: 273, pl. 42 (fig. 3), pl. 46 (figs 1–3)) has described a series of specimens from the Lower Santonian of Hokkaido, Japan, which shows developmental stages at much smaller sizes than seen in the Austrian

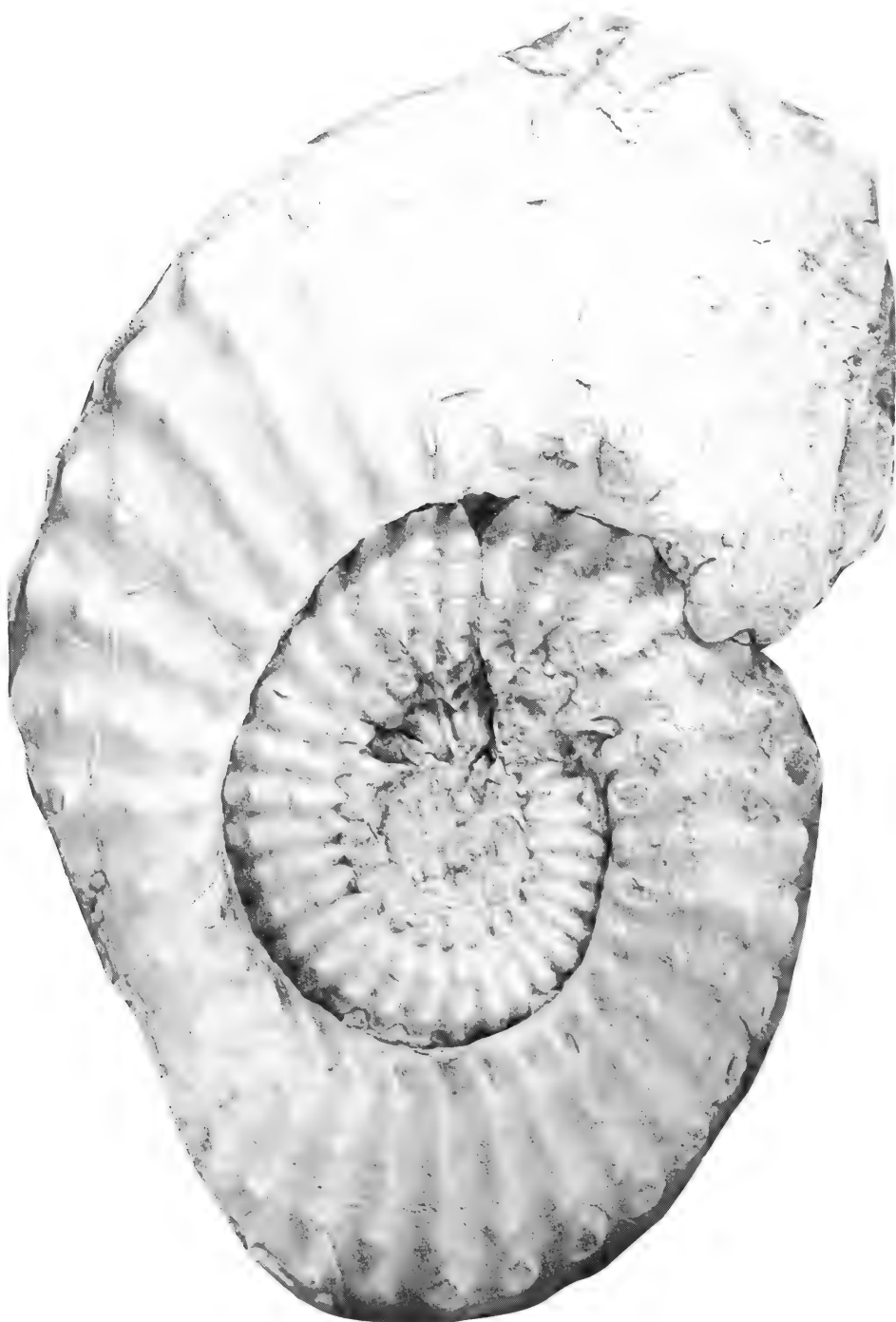


Fig. 8. *Texanites quinquenodosus* (Redtenbacher). The lectotype, GBA 1873/01/13, the original of Redtenbacher 1873, pl. 24 (fig. 3a) from the Santonian Gosau Beds of St Wolfgang, Austria. $\times 1$.

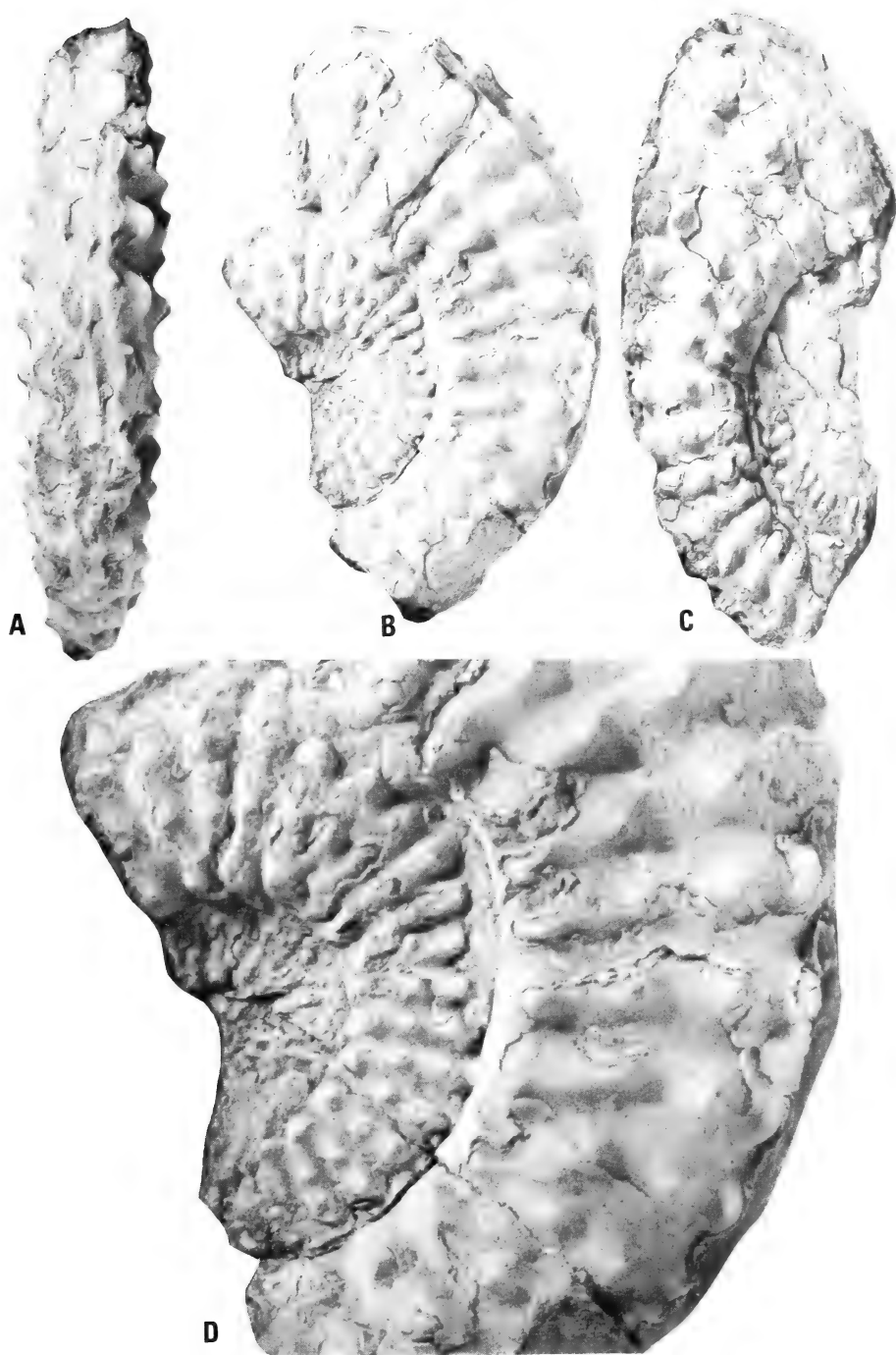


Fig. 9. *Texanites quinquenodosus* (Redtenbacher). Paralectotype, GBA 1873/01/13 (SV 2569), the original of Redtenbacher 1873, pl. 24 (fig. 3a-b) from the Santonian Gosau Beds of St Wolfgang, Austria. A-C $\times 1$; D $\times 2$.



Fig. 10. *Texanites quinquenodosus* (Redtenbacher). A-C. NHMW 1935. III. 41, from the Santonian Gosau Beds of Gosau, Austria. $\times 1$.

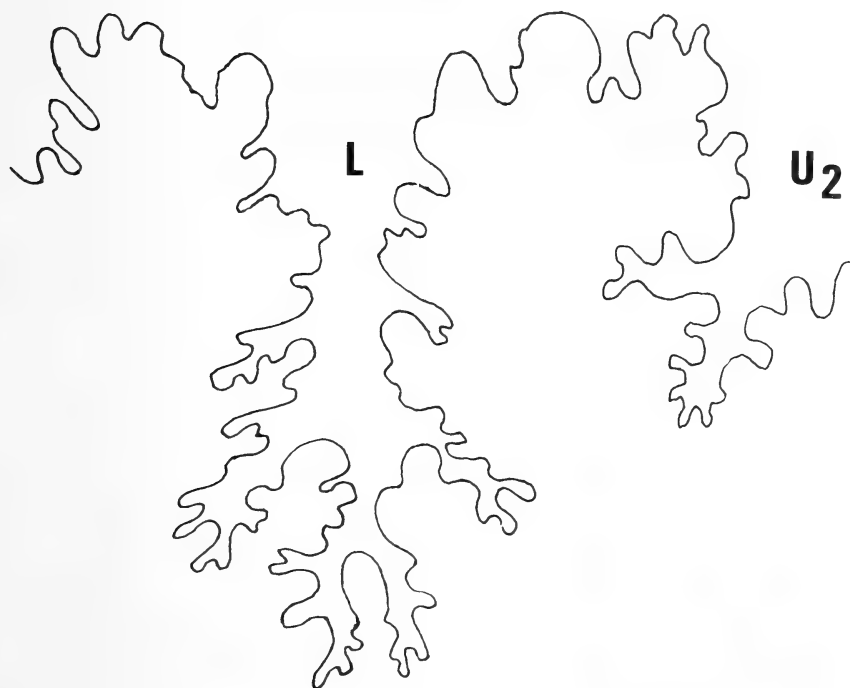


Fig. 11. *Texanites quinquenodosus* (Redtenbacher). External suture of GBA 1873/01/13 (SV2569). $\times 6$.

material. The large specimens from Japan are said to differ from the lectotype in having the ventral (=external (5)) clavus displaced in front of the outer ventrolateral, but this is seen to some degree in GBA 1873/01/13 (SV 2569) (Fig. 9A–B, D), and is probably of limited significance.

Texanites quinquenodosus most closely resembles *Texanites collignoni* Klinger & Kennedy, 1980a (= *Texanites oliveti* non Blanckenhorn sensu Collignon 1948, 1966; Matsumoto & Ueda 1962; Pop & Szasz 1973; Matsumoto 1978) from the Lower Santonian of Madagascar, Zululand, Japan, Romania, and possibly North America. The two species have comparable dimensions and rib densities on the outer whorls, but differ mainly in details of ornamentation. In *T. quinquenodosus* tuberculation is distinctly clavate, especially in the early stages of growth, whereas *T. collignoni* has more spinose ornament throughout. Furthermore, crowding of ribbing and decline of tuberculation towards the body chamber is not as common in *T. collignoni* as in *T. quinquenodosus*. Given more material with precise stratigraphic data, and taking the effects of differential preservation and intraspecific variation into account, specific separation of the two may prove unnecessary. For the present, however, the clavate tuberculation in *T. quinquenodosus* is regarded as being sufficient to separate it from *T. collignoni*.



Fig. 12. *Texanites quinquenodosus* (Redtenbacher). NHMW 1935. III.40, from the Santonian Gosau Beds of Gosau, Austria. $\times 1$.



Fig. 13. *Texanites quinquenodosus* (Redtenbacher). NHMW 1935.III.40, from the Santonian Gosau Beds of Gosau, Austria. $\times 1$.

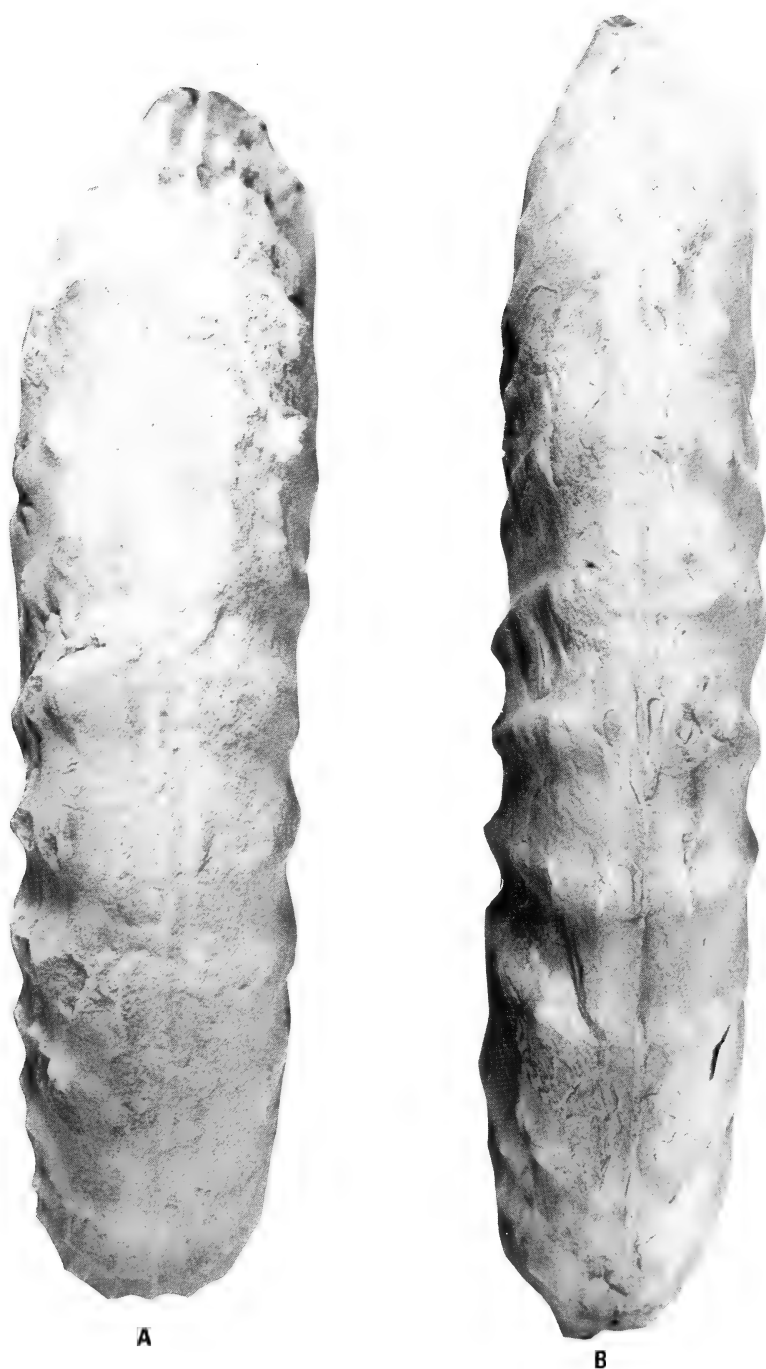


Fig. 14. *Texanites quinquenodosus* (Redtenbacher). A. NHMW 1935.III.40, from the Santonian Gosau Beds of Gosau. B. Paralectotype, LL 41/1938, from Schneiderwirtsbrücke Ischl. A. $\times 1$; B $\times 0,75$.



Fig. 15. *Texanites quinquenodosus* (Redtenbacher). Paralectotype LL 41/1938, from the Santonian Gosau Beds of Schneiderwirtsbrücke, Ischl. $\times 0,75$.

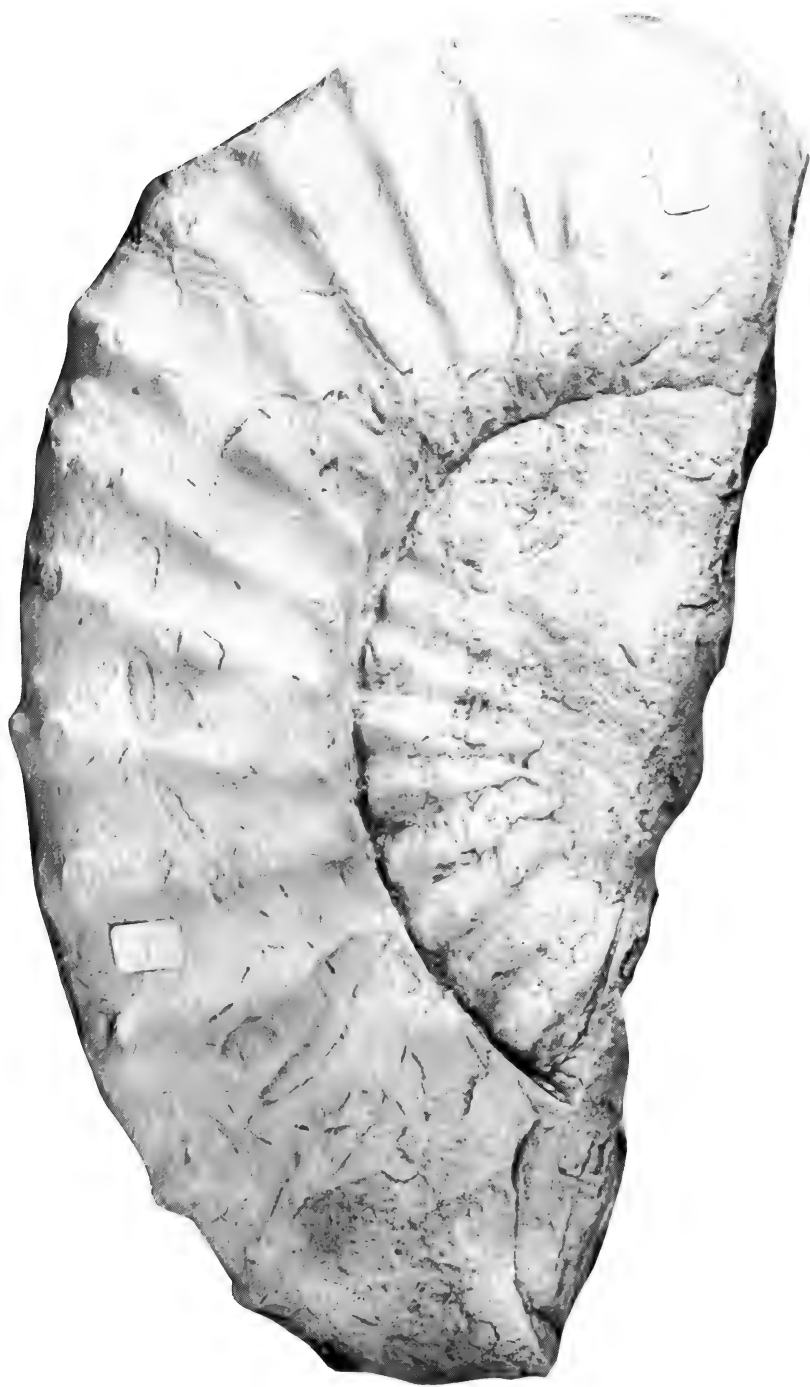


Fig. 16. *Texanites quinquenodosus* (Redtenbacher). Paralectotype, LL 41/1938, from the Santonian Gosau Beds of Schneiderwirtsbrücke, Ischl. $\times 0,75$.

Texanites oliveti (Blanckenhorn, 1905), according to the interpretation of Klinger & Kennedy (1980a), is a distinctly compressed, Upper(?) Santonian species.

T. quinquenodosus may be separated from *Texanites texanus texanus* (Roemer) (see Young 1963: 80, pl. 38 (figs 1–2), pl. 40 (figs 1–3), pl. 41 (fig. 4), text-figs 21g, 22a, 25d) by its more evolute coiling and denser ribbing; these also distinguish it from *T. texanus twiningi* Young (1963: 82, pl. 38 (fig. 5), pl. 39 (fig. 1), pl. 41 (figs 2,5), pl. 48 (fig. 4)). *Texanites texanus gallicus* Collignon (1948: 75, pl. 8 (fig. 1–1a); De Grossouvre 1894: 80, pl. 16 (figs 2, 3a–b, 4a–b), pl. 17 (fig. 1)) is less compressed, and has the inner three rows of tubercles rounded. In *T. texanus hispanicus* Collignon (1948: 76, text-fig. 11–11a, pl. 8 (fig. 2–2b)) there are comparable differences, and the lateral tubercle migrates ventrally until it reaches a mid-flank position.

The Angolan *Texanites quinquenodosus evolutus* Haas (1942: 18, text-fig. 12) has an umbilical diameter of 53 per cent compared to 43 in the best preserved Gosau specimen, and can only very doubtfully be referred to Redtenbacher's species. Similarly, the specimen described as *T. quinquenodosus* from Madagascar (Collignon 1966: 128, pl. 510 (fig. 2021)) is a doubtful representative by virtue of its tighter coiling and more compressed whorl section.

Occurrence

The Austrian specimens can be dated no more precisely than Santonian in our present state of knowledge. The species is also recorded from the Lower Santonian of south-eastern France, Hokkaido (Japan) and, doubtfully, from the Santonian of Angola and Upper Santonian of Madagascar.

INTRASPECIFIC VARIATION IN *Reginaites zulu*

KLINGER & KENNEDY, 1980, AND HOMOEOMORPHY WITH
Plesiotexanites (*P.*) *stangeri* (BAILY, 1855)

(By H. C. Klinger & W. J. Kennedy)

In the authors' (Klinger & Kennedy 1980a) description of the South African representatives of the ammonite subfamily Texanitinae, two new species definitely referable to the genus *Reginaites* Reymont, 1957, were erected: *Reginaites zulu* and *Reginaites reymonti*.

Recent collecting at the type locality of *R. zulu* yielded additional material that allows the authors to comment on the intraspecific variation in the species and firmly to date it as Upper Santonian on the basis of its association with *Inoceramus* (*Cordiceramus*) *muelleri* Petrascheck. It also demonstrates a striking homoeomorphy with the partly contemporary (though apparently geographically separated) species *Plesiotexanites* (*P.*) *stangeri* (Baily, 1855). The

material further supports the authors' inclusion of *Reginaites* in the subfamily Texanitinae, rather than in the subfamily Peroniceratinae Hyatt, as advocated by Matsumoto (1965: 238) and Wiedmann (1978: 670).

Reginaites zulu Klinger & Kennedy, 1980

Figs 17–25

Reginaites zulu Klinger & Kennedy, 1980a: 116, figs 90–92, 93A–B, 94.

Types

The holotype by original designation is SAS–H126A/9 from Bed A at locality 105 on the south-eastern shores of False Bay, Zululand, St Lucia Formation, Upper Santonian. Paratype SAS–H126A/4 is from the same horizon and locality.

Material

Five specimens, SAM–PCZ5952–6, all from the same locality and horizon as the types.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>	<i>R</i>
PCZ5955	75,0	25,0(33,3)	26,0(34,7)	0,96	36,0(48,0)	18
at	134,0	34,0(25,4)	35,0(26,1)	0,97	74,0(55,2)	11 × 2
PCZ5953	120,0	32,0(26,7)	34,0(28,3)	0,94	62,0(51,7)	23
H126A/9	140,0	38,7(27,6)	40,0(28,6)	0,96	74,0(52,9)	21
PCZ5956	195,0	—	56,0(28,7)	—	105,0(53,8)	—

Description

Coiling is very evolute with an umbilical diameter varying between 48 and 55 per cent, increasing with growth. The whorl section changes through ontogeny, being subsquare on the inner whorls, becoming compressed subrectangular with a fastigiate venter, and then distinctly compressed with a conspicuous central keel and subordinate lateral keels (Fig. 17A).

None of the specimens has the innermost whorls preserved, but in SAM–PCZ5953 (Fig. 18) ornament at approximately 40 mm diameter already consists of pinched umbilical (1) bullae situated at the umbilical edge, and broad, low, prorsiradiate ribs bearing very large, bullate to clavate elongated ventrolateral (3 + 4) tubercles situated a little distance away from the umbilical seam of the succeeding whorl. The venter at this stage is already distinctly tricarinate, with the central keel strongest. Strength and density of ribbing is extremely variable, as the Figures show.

Division of the ventrolateral tubercle takes place at varying diameters. In SAM–PCZ5953 (Fig. 18) definite signs of division are already present at a diameter of approximately 50 mm, whereas in the holotype this becomes noticeable only at a diameter of 65 mm (Figs 19–20). With increasing diameter

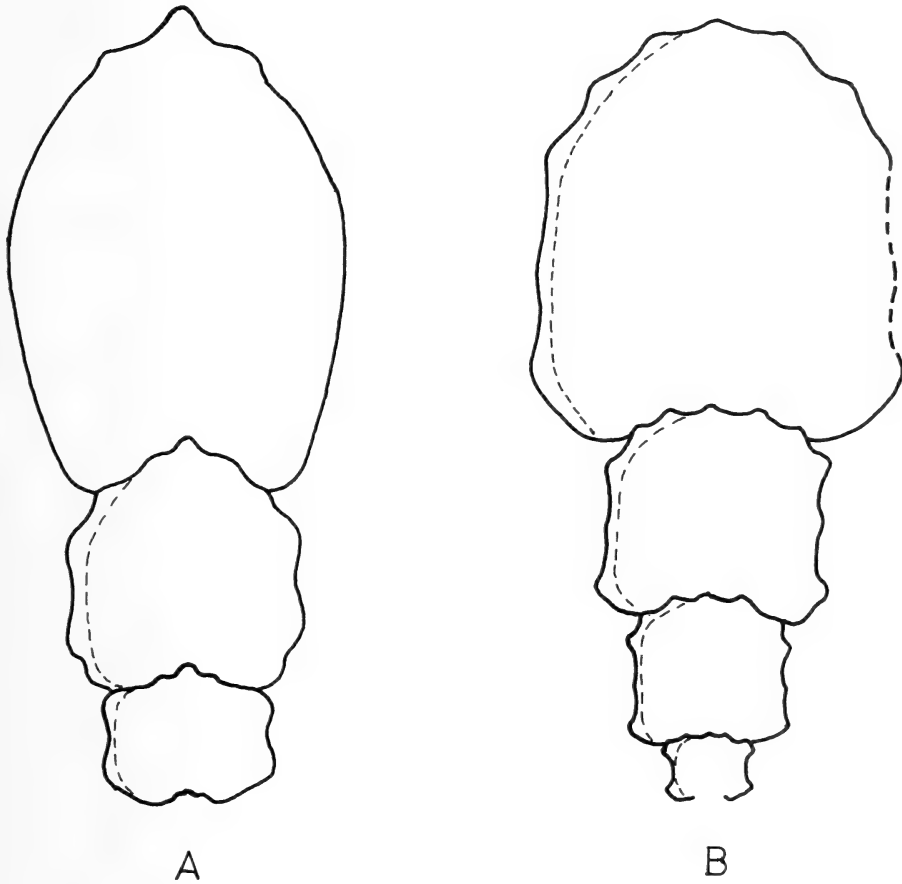


Fig. 17. A. *Reginaites zulu* Klinger & Kennedy, 1980, illustrating ontogenetic changes in whorl section (after Klinger & Kennedy 1980a, fig. 90A). B. *Plesiotexanites* (*P.*) *stangeri* (Baily, 1855) illustrating ontogenetic changes in whorl section (after Matsumoto 1970, text-fig. 23b). All $\times 1$.

this separation becomes more obvious, resulting in a clavate marginal (4) tubercle, situated slightly forward of a larger, rounded submarginal (3) tubercle (Figs 20A–B, 21C–D). Concurrent with division of the ventrolateral tubercle, all lateral ornament weakens, the ratio of whorl breadth to whorl height decreases, and the venter becomes distinctly fastigiate. Differences in strength of ornament and stage at which attenuation takes place is variable. SAM-PCZ5956 (Fig. 22) shows attenuation of ornament and change in whorl section to the point where the flanks of the last part of the phragmocone are smooth. On body chambers (Figs. 21A–B herein) (Klinger & Kennedy 1980a, fig. 94A–B) lateral ornament is reduced to indistinct broad, low swellings.



Fig. 18. *Reginaites zulu* Klinger & Kennedy, 1980. SAM-PCZ5953 from locality 105, St Lucia Formation, Zululand. $\times 1$.

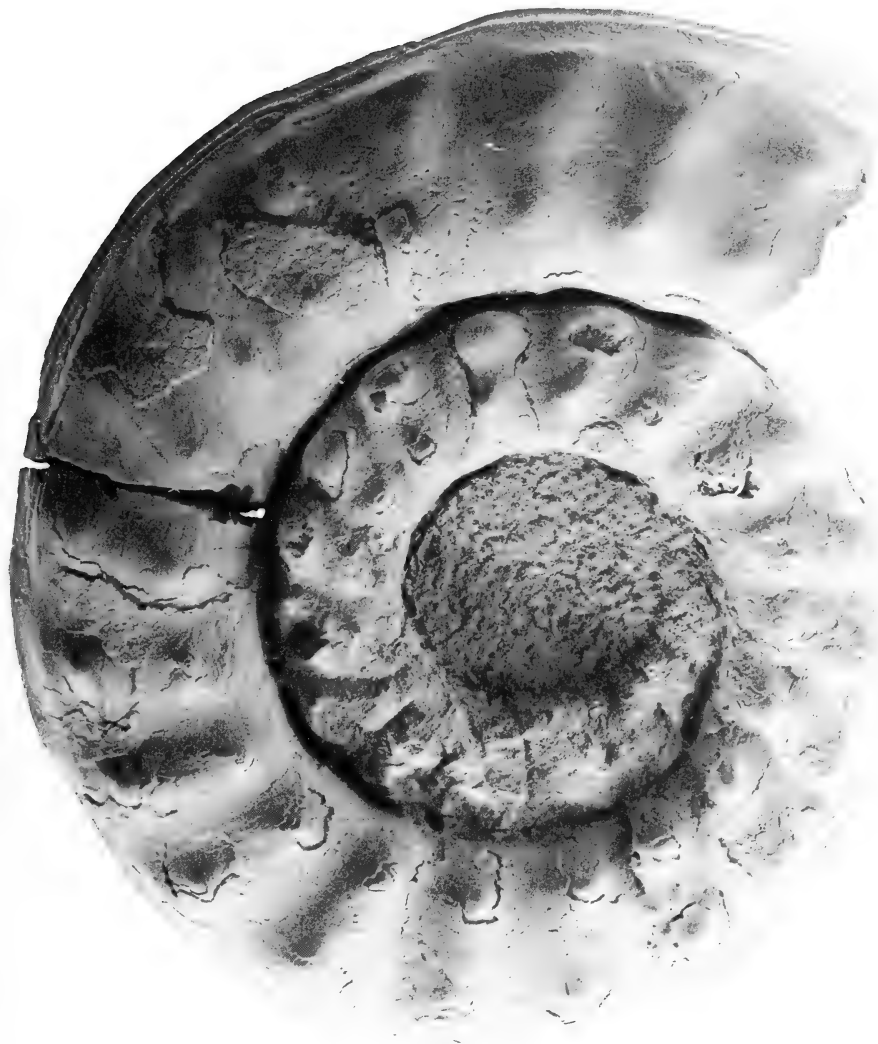


Fig. 19. *Reginaites zulu* Klinger & Kennedy, 1980. The holotype, SAS-H126/9, from locality 105, St Lucia Formation, Zululand. $\times 1$.



Fig. 20. *Reginaites zulu* Klinger & Kennedy, 1980. The holotype, SAS-H126/9, from locality 105, St Lucia Formation, Zululand. $\times 1$.

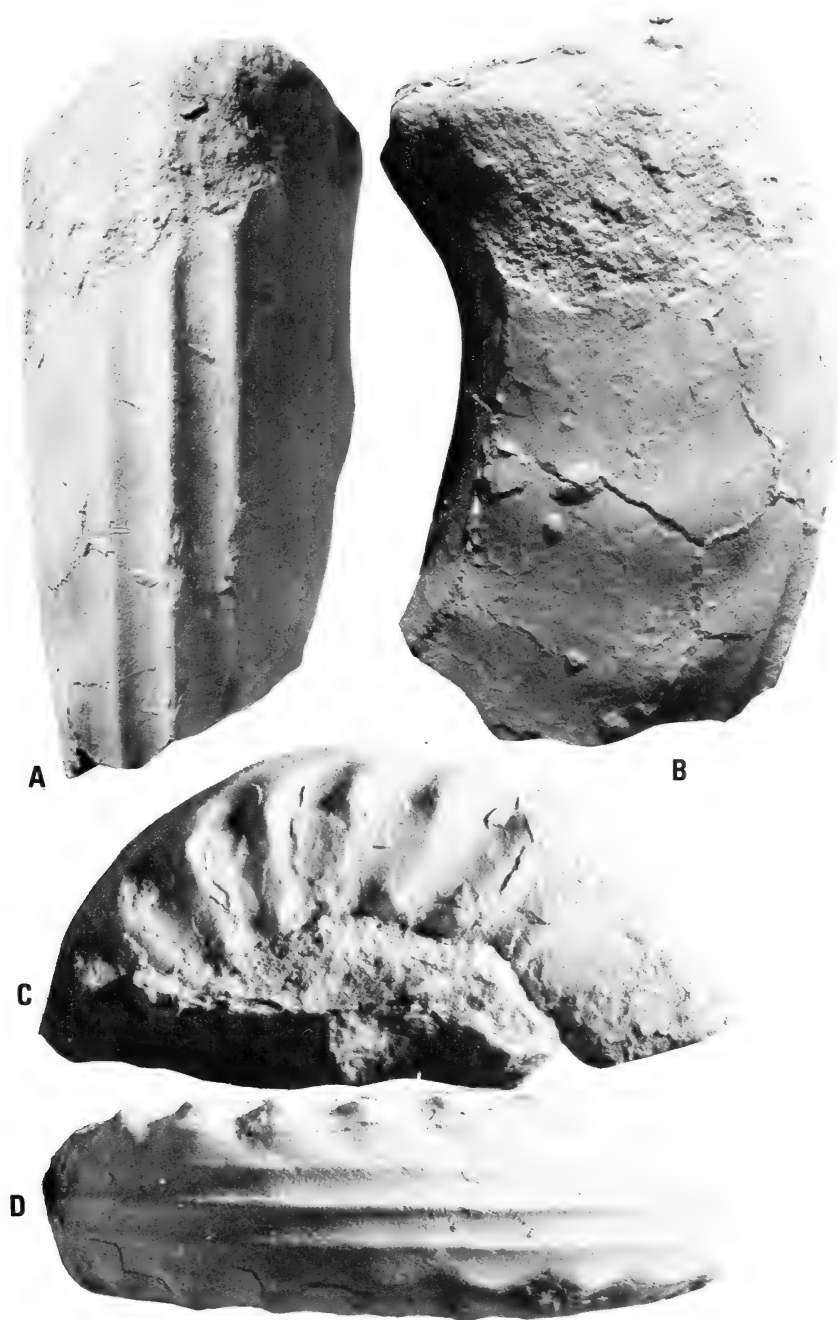


Fig. 21. *Reginaites zulu* Klinger & Kennedy, 1980. A-B. SAM-PCZ5952, a body chamber fragment illustrating total disappearance of ornament. C-D. SAM-PCZ5954 illustrating division of ventrolateral tubercle. Both specimens from locality 105, St Lucia Formation, Zululand. $\times 1$.



Fig. 22. *Reginaites zulu* Klinger & Kennedy, 1980. SAM-PCZ5956 illustrating ontogenetic change in ornament. From locality 105, St Lucia Formation, Zululand. $\times 0,5$.

None of the specimens shows distinct lateral (2) tubercles at any stage of ontogeny, although SAM-PCZ5955 (Fig. 23) has faint swellings on the central part of the ribs on the inner whorls. Preservation is poor, and we cannot confirm that these are incipient lateral (2) tubercles or not. In only three specimens are part of the suture exposed: it is rather simple (Fig. 24) but varies considerably in details and the width of the lateral lobe (L).

Discussion

With only the holotype and a fragment of body chamber of *Reginaites zulu* at their disposal, the authors (Klinger & Kennedy 1980a) were initially

impressed by the strong ornament on the inner whorls of the phragmocone and the lack of ornament on the body chamber, and failed to recognize the resemblance of the species to *Plesiotexanites* (*P.*) *stangeri* (Baily, 1955). The new material shows that there is remarkable similarity, and that the two species may be closer related than previously suspected. (Young 1963: 93 had also



Fig. 23. *Reginaites zulu* Klinger & Kennedy, 1980. SAM-PCZ5955, specimen with sparse costation, comparable with *Plesiotexanites* (*P.*) *stangeri* 'var. *sparsicosta*' Spath. From locality 105, St Lucia Formation, Zululand. $\times 1$.

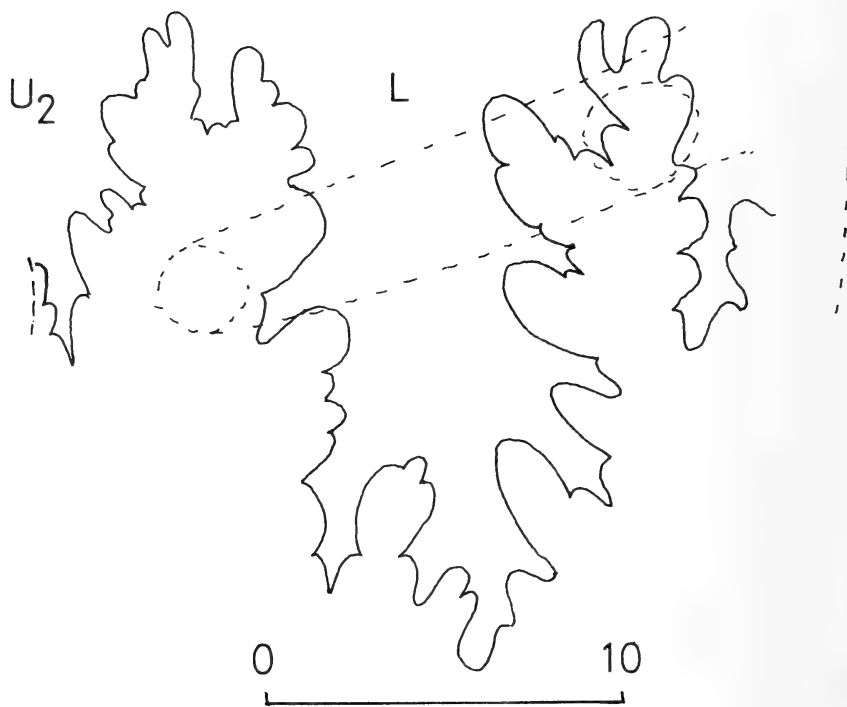


Fig. 24. *Reginaites zulu* Klinger & Kennedy, 1980. Part of external suture of SAM-PCZ5956. Millimetre scale bar for size.

commented on similarities between *Reginaites durhami* Young and *Plesiotexanites* (*P.*) *stangeri*). In addition, this is the largest assemblage of *Reginaites* known, most other species being monotypic.

The ontogenies of *R. zulu* and *P. (P.) stangeri* are very similar, although the accompanying changes in ornament and whorl section are much more strongly expressed in the former. These changes involve development of tuberculation on the inner whorls, gradual effacement of all ornament on the outer phragmocone whorls and body chamber, and change in whorl section.

In the very early stages, *R. zulu* and *P. (P.) stangeri* differ only in ventral ornament. *R. zulu* is distinctly tricarinate, whereas *P. (P.) stangeri* is unicarinate, with a pair of spirally elongated external (5) tubercles.

In both species the ventrolateral (3 + 4) tubercle, which is situated in the umbilical seam, is enlarged in *Protexanites* (*Protexanites*) fashion in early stages of growth. At varying diameters this ventrolateral tubercle starts dividing into two, resulting in a clavate marginal (4) and a generally rounded submarginal (3) tubercle—the so-called '*Parabevahites*' stage. The *Paratexanites*-like stage, in which total separation of these tubercles takes place, is completed in both species, generally with the marginal (4) tubercle situated slightly ahead of the



Fig. 25. *Plesiotelexites* (*P.*) *stangeri* (Baily, 1855). Cast of holotype, BMNH C73333, from Umzamba estuary, Pondoland. $\times 0,43$.

submarginal (3) one. While the separation of the ventrolateral tubercle takes place in *P. (P.) stangeri*, a lateral (2) tubercle appears, thus completing the pentatuberculate *Texanites*-like stage. The stage of appearance, strength and persistence of the lateral (2) tubercle in *P. (P.) stangeri* is very variable. The lateral tubercle may be faint throughout, or persist only for a short time before being absorbed into the ribbing. As far as *lateral* ornament is concerned, the only difference between *P. (P.) stangeri* and *R. zulu* is the variable appearance

of a lateral (2) tubercle in the former. The venters, however, remain different throughout.

Apart from relative strength of ornament at comparable stages of development (which may partially be explained by differential preservation), *R. zulu* and *P. (P.) stangeri* show comparable intraspecific variation in density of ribbing, which has led to the usage of varietal names *sparsicosta* and *densicosta* in the latter species (e.g. Spath 1921: 138, pl. 5 (figs 1–2)). In *P. (P.) stangeri* these differences in density of ribbing appear to be restricted mainly to the inner whorls, whereas in *R. zulu* they are noticeable to greater diameters.

In both species ornament weakens during ontogeny, although the reduction is more prominent in *R. zulu* than in *P. (P.) stangeri*. The new material referable to *R. zulu* (Fig. 22) shows that parts of the phragmocone may already be devoid of ornament, whereas the body chamber is completely smooth, except for low, broad, undulating swellings (Fig. 21A–B herein) (Klinger & Kennedy 1980a Fig. 94A–B). In *P. (P.) stangeri* a similar weakening takes place, but in the holotype the largest specimen as yet obtained of the species, the body chamber (which consists of one whorl here) still bears faint, though discernible lateral ornament (Fig. 25).

There are also comparable ontogenetic changes in whorl section (Fig. 17A–B). Both species are initially depressed, quadrate to rectangular, but whorl height gradually increases over whorl breadth, so that the section is eventually distinctly compressed. The venter becomes fastigate in both species, but in *R. zulu* this is enhanced by the lateral keels.

Phylogenetic relationships between *R. zulu* and *P. (P.) stangeri* are not clear, but the ontogenetic changes in both species are too similar to consider them to be entirely those of homoeomorphs. *P. (P.) stangeri* occurs mainly in the Upper Santonian of Pondoland, but has also been recorded from the Middle Santonian of Madagascar, and Young (1963: 22) even records it as early as the lowest parts of the Lower Santonian of the Gulf Coast of North America. *R. zulu* occurs in Zululand in association with *Inoceramus (Cordiceramus) muelleri* Petrascheck, but below the first occurrence of *Submortoniaceras*, which places it in the uppermost part of the Santonian. Because of similarities of ornament on the inner whorls of *R. zulu* and *Plesiotexanites (P.) matsumotoi* Klinger & Kennedy, 1980a, it seems feasible to derive *R. zulu* from the latter (probably via *Reginaites reymonti* Klinger & Kennedy, 1980a) in the Upper Santonian, rather than directly from *P. (P.) stangeri*. However, the parallel changes in ontogenetic development of *R. zulu* and *P. (P.) stangeri* are so striking that we can perhaps trace their ancestry to a common origin somewhere in the Lower Santonian.

Palaeobiogeographic data should be interpreted with caution on the basis of this limited material but, to date, the great majority of specimens of *P. (P.) stangeri* have been reported from the transgressive shallower water sediments of the Umzamba Formation, whereas all known specimens of *R. zulu* have been found in the deeper water sediments of the St Lucia Formation of Zululand.

Differences between *R. zulu* and other species of *Reginaites* were given earlier (Klinger & Kennedy 1980a), and are here briefly repeated: *R. quadratuberculatum* Reyment, 1957, *R. leei* (Reeside, 1927), *R. durhami* Young, 1963, *R. reymonti* Klinger & Kennedy, 1980a, and *R. gappi* Wiedmann, 1978, all have a lateral tubercle at some stage. '*Reymentites*' *hatai* Matsumoto, 1965, has the umbilical tubercle displaced on the flanks.

All these data support the authors' (Klinger & Kennedy 1980a) and Young's (1963) views of placing the genus *Reginaites* in the subfamily Texanitinae, rather than in the subfamily Peroniceratinae.

COLOUR-BANDING IN MICROMORPHS OF *Submortonicerases woodsii*
(SPATH, 1921) AND THEIR HOMOEOMORPHY WITH *Protexanites*
(*P.*) *bontanti shimizui* MATSUMOTO, 1970.

(By H. C. Klinger & W. J. Kennedy)

Two small specimens of *Submortonicerases woodsii* from the Santonian-Campanian sediments of Kwa-Mbonambi, Zululand (locality 6 of Kennedy & Klinger 1975: 282) are of interest in showing traces of colour bands in the preserved part of the shell, and in apparently being adult at diameters well below those of normal representatives of the species. They also show striking homoeomorphy with the stratigraphically older *Protexanites* (*P.*) *bontanti shimizui* Matsumoto, 1970.

Submortonicerases woodsii s.l. (Spath, 1921)

Figs 26-27

Submortonicerases woodsii s.l. (Spath): Klinger & Kennedy, 1980a: 242, figs 186-199, 200B (with synonymy).

Material

SAM-PCZ5957-8 both from an unspecified horizon near the Santonian-Campanian boundary at Kwa-Mbonambi (locality 6 of Kennedy & Klinger 1975: 282), St Lucia Formation, Zululand.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
PCZ5957	46,0	13,5(34,0)	18,5(40,2)	0,73	15,0(32,6)
PCZ5958 (crushed)	48,0	12,5(26,0)	17,0(35,4)	0,73	—

Description

Both specimens are less than 50 mm in diameter. PCZ5958 is crushed dorsoventrally, hence the umbilicus appears much narrower than that of PCZ5957.

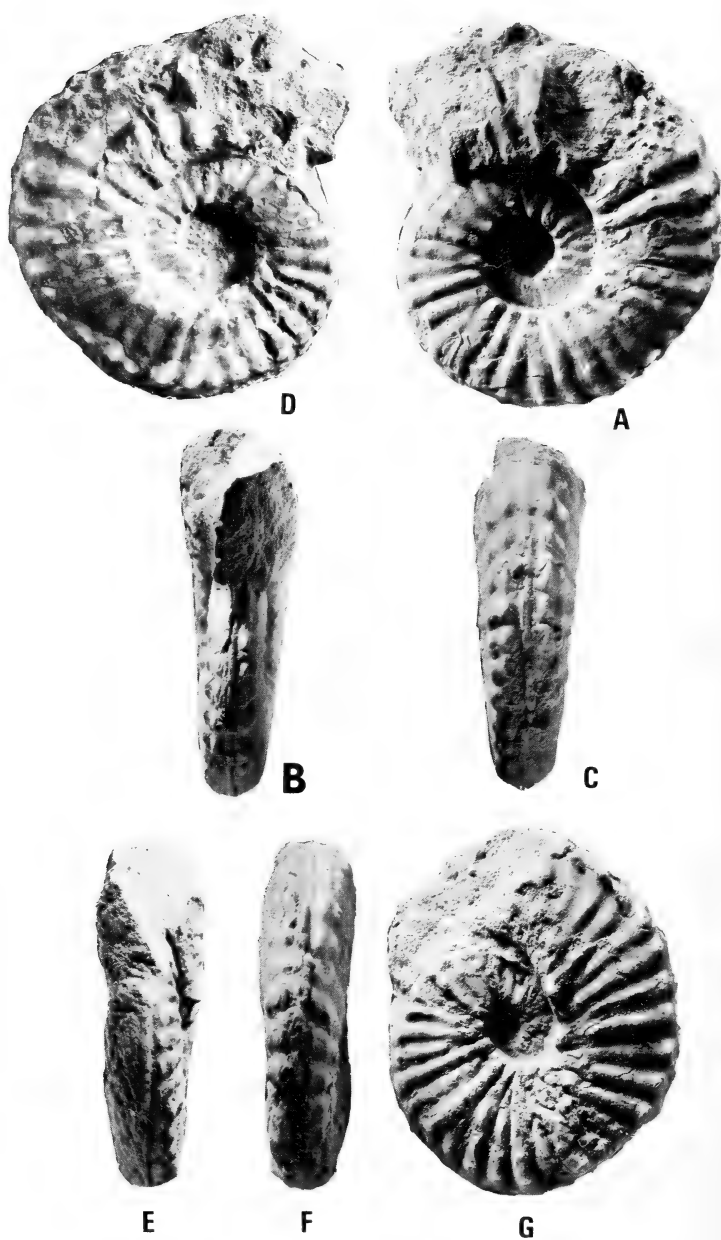


Fig. 26. *Submortoniceras woodsi* (Spath, 1921). A-D. SAM-PCZ5957. D without whitening to show parts of colour banding. E-G. SAM-PCZ5958, specimen crushed dorsoventrally. Both from locality 6, St Lucia Formation, Zululand. All $\times 1$.

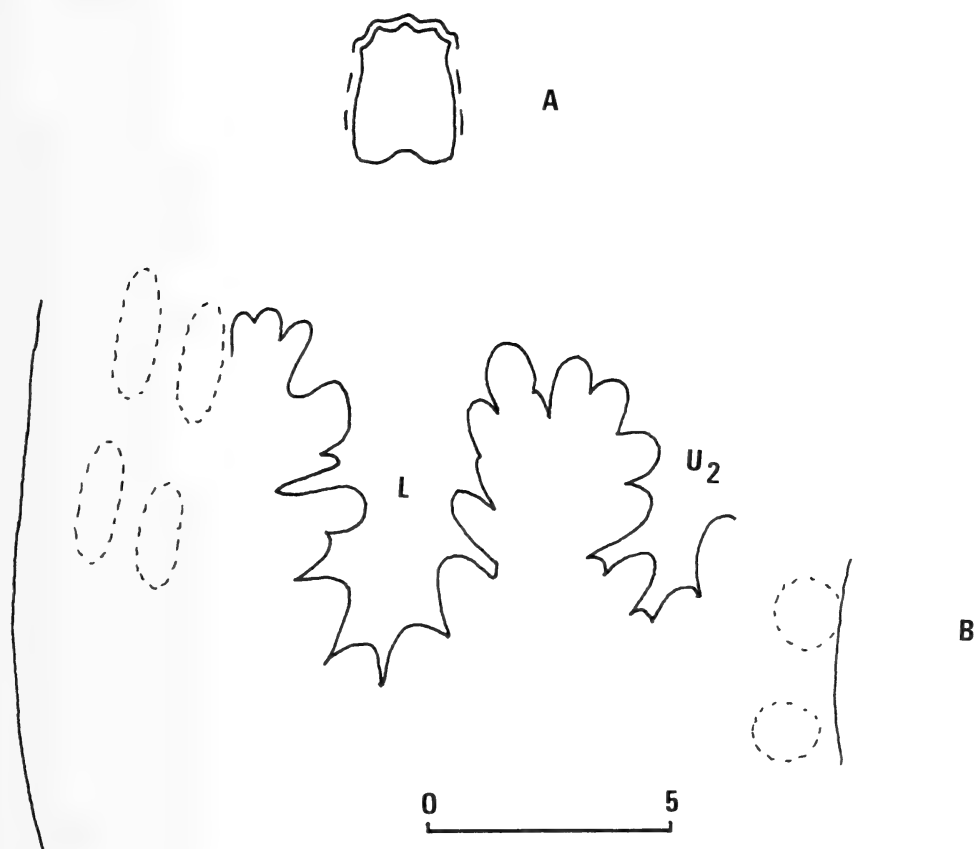


Fig. 27. *Submortoniceras woodsi* (Spath, 1921). A. Whorl section of SAM-PCZ5957 to illustrate distribution of colour banding, $\times 1$. B. External suture of SAM-PCZ5956, millimetre scale bar for size.

PCZ5957 (Fig. 26A–D) shows details of the ontogeny. At 5 mm diameter the flanks are still completely smooth; at 8 mm diameter umbilical (1) tubercles and bifurcating ribs are visible on the flanks. At 16 mm diameter weak lateral (2) and submarginal (3) tubercles appear on the flanks. A full texanite complement of 5 rows of tubercles and a median keel is visible at 25 mm diameter. The lateral (2) and submarginal (3) tubercles, however, are very weak, mimicking a *Protexanites* (*P.*)-like type of ornament. Ornament remains like this until near the apertural end, where the lateral (2) tubercle becomes slightly more prominent. The last half-whorl is non-septate and the last few septa overlap.

Part of the original aragonitic shell material is preserved. The inner shelly layer is creamy coloured with a reddish tint, whereas the outer layer is more

brownish. On the outer layer, two darker, sepia-coloured spiral bands are visible, one near the submarginal (3) tubercle (Fig. 26D). In addition, a distinct black substance occurs in the ventral area between the opposite rows of marginal (4) and external (5) tubercles in places. The distribution of colour bands is shown in Figure 27A.

PCZ5958 (Fig. 26E–G) is not as well preserved, but shows distinct pentatuberculate ornament at 25 mm diameter. The lateral (2) and submarginal (3) tubercles are again weaker than the others. Ornament weakens towards the later part of the phragmocone, but again becomes stronger on the body chamber. The last few septa are also crowded.

Discussion

Because of the weak development of the lateral (2) and submarginal (3) tubercles, and also because of the small size, these specimens are striking homoeomorphs of the stratigraphically older *Protexanites* (*P.*) *bontanti shimizui* Matsumoto, 1970 (compare Matsumoto 1970, pl. 31 (figs 1–2), text-fig. 6; 1971: 147, pl. 23 (fig 4), text-fig 10; Matsumoto & Hirano 1976: 335, pl. 35 (figs 1–4), text-fig. 2). Close examination, however, clearly shows the pentatuberculate ornament in the Zululand specimens. The two species also differ considerably in details of the suture lines (compare Fig. 27B herein with Matsumoto 1970, text-fig. 6) and cannot be confused with each other. Examination of the suture lines in the present material suggests closest affinity with the subspecies *Submortonicerias woodsi woodsi* as interpreted by Klinger & Kennedy (1980a: 252–3).

Matsumoto (1970: 238) had already commented on the similarity between *Protexanites* (*P.*) *bontanti* s.l. and some examples of *Submortonicerias*, e.g. *S. collignoni* (Shimizu); the latter a possible synonym of *S. woodsi* according to the authors (Klinger & Kennedy 1980a: 238). Matsumoto's observations are further enhanced by the present data.

The presence and distribution of the colour bands on the one specimen, PCZ5957, compares favourably with that described in *P. (P.) bontanti shimizui* by Matsumoto & Hirano (1976) and adds to the homoeomorphic resemblance. Unfortunately, our material is too poorly preserved to add to Matsumoto & Hirano's general comments on coloration in Texanitinae, but nevertheless represents yet another record of coloration in the subfamily.

The ontogenetic changes in ornament and the crowding of the last few septa suggest that these two specimens represent adult individuals. The question that now arises is the relationship of these micromorphs to the more commonly known large specimens (even the specimen considered as dwarfed by the authors (Klinger & Kennedy 1980a figs 198, 200B) is gigantic compared to the present material). If nutritional deficiency were to blame (compare Boletzky & Wiedmann 1978), the co-occurrence of 'normally sized' specimens, e.g. SAM-PCZ5897 (Klinger & Kennedy 1980a, fig. 192) at 226 mm diameter at the same locality would be a contradiction. Apart from differences in overall

size, the present specimens differ from contemporary *S. woodsi* only in having a lower whorl section, as comparison of dimensions shows:

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>	<i>U:Eths</i>
PCZ5897	226.0	74.0(32.7)	92.0(40.7)	0.80	74.0(32.7)	25 : 34
PCZ5957	46.0	13.5(34.0)	17.0(35.4)	0.73	15.0(32.6)	26 : 36

It is possible that we are here dealing with sexual dimorphs, the 'normally sized' specimens being the female (macroconch) and the smaller form the male (microconch). Apart from the fact that this would be the first suggestion of sexual dimorphism in the ammonite subfamily Texanitinae, the implications on the systematics, especially in the genus *Submortonicer*, are disturbing. Matsu-moto (1959) and Klinger & Kennedy (1980a) have illustrated the bewildering extent of intraspecific variation in *Submortonicer chicoense*, and *S. woodsi* and *S. condamyi* respectively. Added to this is a very rapid rate of evolution, as exemplified by *S. woodsi* and *S. condamyi*, which makes it difficult to separate one chronospecies satisfactorily from another. Should sexual dimorphism be added to the list of variables in the systematics of the genus *Submortonicer*, global correlation may become even more tenuous than at present.

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

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Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Capital initial letters

- The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
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CRETACEOUS FAUNAS FROM
ZULULAND AND NATAL, SOUTH AFRICA
ADDITIONAL OBSERVATIONS ON THE
AMMONITE SUBFAMILY TEXANITINAE
COLLIGNON, 1948

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ANNALS

OF THE SOUTH AFRICAN
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CAPE TOWN



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KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* 17 (4): 1-51.

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(continued inside back cover)

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OCCLUSAL MORPHOLOGY
OF THE MANDIBULAR PERMANENT MOLARS
OF THE SOUTH AFRICAN NEGRO AND
THE KALAHARI SAN (BUSHMAN)

By

F. E. GRINE

Cape Town Kaapstad

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By

F. E. GRINE

South African Museum, Cape Town

(With 8 figures and 26 tables)

[MS accepted 2 July 1981]

ABSTRACT

A number of morphological crown variants are investigated. These features include the principal cusp number, the tuberculum sextum and tuberculum intermedium, the configuration of the primary occlusal pattern, the mesial and distal foveae, the deflecting wrinkle, and the appearance of the occlusal enamel. The definitions and the various methods employed in the classification of these characters are reviewed. The amount and degree of significant sexual dimorphism of these crown variants are low in both the San and Negro. Significant interpopulation differences in these features are more common. The fovea anterior and tuberculum sextum appear to be the most useful discriminatory characters, while the second molar displays the greatest number of significant differences between the San and Negro. A characterization of the lower molar morphology of the San and Negro is provided. Paired chi-square evaluations of various characters showed most to be independent of one another. The dental data provided here for the San and the South African Negro are compatible with, and to some degree corroborate what is known about, the interrelationships of these peoples from non-dental morphological and genetic data.

CONTENTS

	PAGE
Introduction	158
Material and methods	158
Definition and classification of morphological features	162
Principal cusp number	162
Tuberculum sextum	163
Tuberculum intermedium	163
Primary occlusal pattern	164
Deflecting wrinkle	168
Fovea anterior and posterior	170
Enamel wrinkling	172
Results	172
Discussion	199
Sexual dimorphism	199
Characteristics of San and Negro molars	200
Occlusal morphological interrelationships	202
Biological interrelationships of the South African Negro and the Kalahari San	203
Summary	207
Acknowledgements	208
References	209

INTRODUCTION

The human mandibular molar presents a number of features that are of importance in both anthropological and palaeoanthropological contexts. These occlusal characters have been recorded extensively in both recent and fossil representatives of hominid populations, and they have been used to quantify both interracial and population differences as well as evolutionary trends.

Amongst the numerous minor morphological variants that can be examined, several have been shown to have considerable theoretical potential as anthropological markers. These features are: (i) the principal cusp number, (ii) the presence or absence of the tuberculum sextum, (iii) the presence or absence of the tuberculum intermedium, (iv) the form of the primary occlusal pattern, (v) the presence or absence of a deflecting wrinkle, (vi) the presence or absence of the mesial and distal foveae, and (vii) the appearance of the enamel (smooth or crenulate).

The purpose of this paper is to provide information on the morphology of the lower permanent molars of two populations, the South African Negro and the Kalahari San (Bushman), for which the majority of these characters have heretofore not been recorded. Previous investigations of these populations have been restricted to the detailing of cusp number (Shaw 1927; Drennan 1929; Oranje 1934) or of the primary cusp and groove pattern (Kiernberger 1955; Van Reenen 1966; Jacobson 1967). Morris (1970) presented data on the frequency of the metaconid deflecting wrinkle on the first molars only.

Although these characters have been described and documented extensively in the literature, there remains a fundamental lack of consensus amongst workers on the classification and interpretation of several of these features. This lack of agreement presents one of the major obstacles which preclude comparisons between results reported in the various studies of these features in recent human populations.

Thus, in addition to providing information on the morphology of the South African Negro and San lower molar, the problems of definition and classification of these characters will also be considered in the hope that a workable series of models might be developed.

MATERIAL AND METHODS

The dentitions examined are drawn from the Khoisanoid and Negroid populations of southern Africa. The Negroid sample comprises skulls of South African Bantu-speaking Negroes housed in the Raymond A. Dart Collection of Human Skeletons, Department of Anatomy, University of the Witwatersrand. The skeletal material housed in this collection has been prepared from dissection-hall subjects and, thus, the sex of each individual is known and the tribal group is known for most. The Negro mandibles examined here were drawn from the following tribal groups: Natal Nguni (Zulu and Swazi), Cape Nguni (Xhosa and Pondo), Sotho (Sotho and Tswana), and Shangana-Tonga

(Shangaan and Tonga). The major group only (e.g. Natal Nguni, Sotho) was recorded for each individual because De Villiers (1968) has shown through analyses of skull variability that there are no distinguishing intertribal differences.

Although some of the material housed in the Raymond A. Dart Collection is probably derived from individuals who lived on the Witwatersrand for perhaps their entire lives, or at least prior to their deaths, some (or their parents) had moved to the Witwatersrand from their 'traditional' tribal areas. The geographical distribution of the tribal groups from which material was selected for study is shown in Figure 1. The numbers of individuals derived from each group are recorded in Table 1. A total of 506 Negro dentitions (353 male and 153 female) was examined.

The term San, rather than Bushman, is used in this study as the former is taken to denote a biological entity whereas the latter refers more precisely

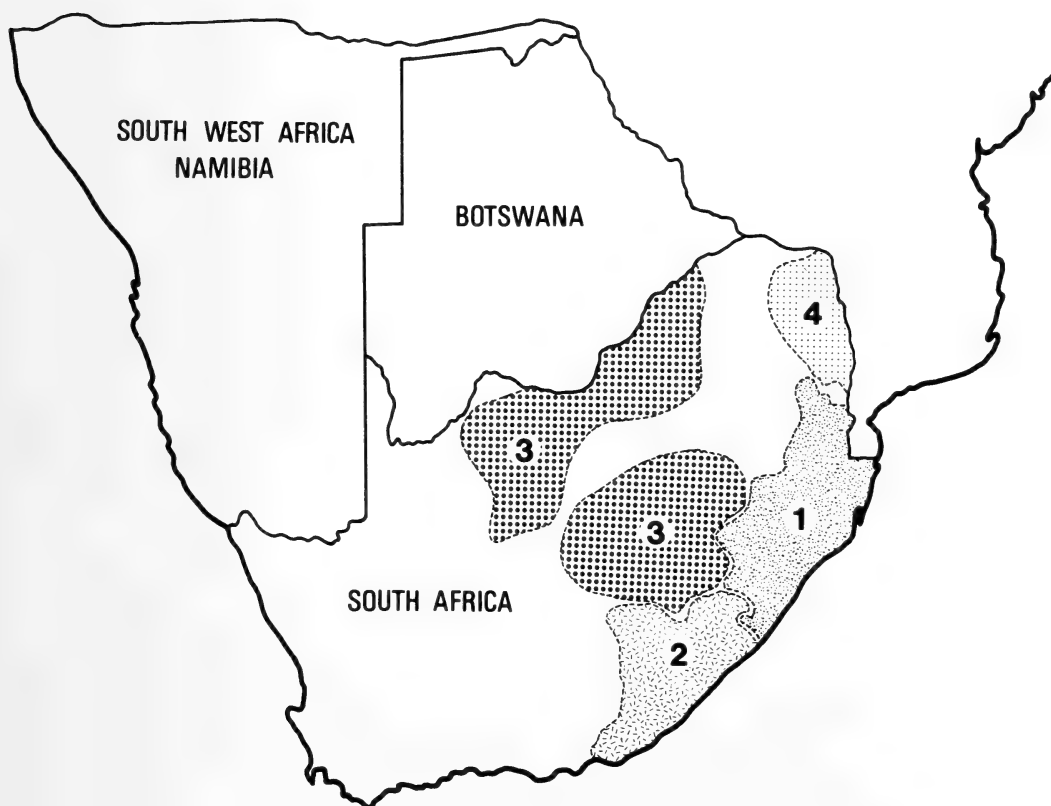


Fig. 1. Distribution of the South African Negro population groups sampled in the present study. 1—Natal Nguni, 2—Cape Nguni, 3—Sotho, 4—Shangana-Tonga (adapted from Lawton 1967).

to the linguistic and ethnological practices of these people (Jenkins & Tobias 1977; Tobias 1978).

TABLE 1
Number of Negro and San individuals examined.

<i>Population</i>	<i>Tribal or linguistic group</i>	<i>Male</i>	<i>Female</i>	<i>Total</i>
Negro	Natal Nguni	111	60	171
	Cape Nguni	90	34	124
	Sotho	99	55	154
	Venda	21	3	24
	Shangana-Tonga	32	2	34
		353	154	507
San	Nharo	16	14	30
	G/wi	6	3	9
	'Tshu-Khwe'	8	2	10
	≠kxʰao//ʰǃ	5	5	10
	!xóǀ	15	21	36
	Unspecified	66	64	130
		116	109	225

The San sample is comprised of plaster casts made from impressions of living subjects taken by Van Reenen and his co-workers on three separate trips to the Kalahari in 1958, 1959, and 1964 (Van Reenen 1966). The sex of each individual is known, and the 'tribal' group was recorded for a number of the subjects.

The San populations recorded are drawn from the Northern, Central and Southern Bush linguistic groups. The Nharo and G/wi form a homogeneous linguistic group which Bleek (1927) termed the Central Bush language group. Westphal (1963) renamed this unit the Tshu-Khwe linguistic family. Some ten individuals (eight males and two females) were recorded in the field notes as 'Tshu-Khwe', and although this is not properly a 'tribal group' it is indicated in Table 1 as a population. The ≠kxʰao//ʰǃ belong to the Northern Bush (Bleek 1927) or Zhu (Westphal 1963) language group, and the !xóǀ are considered to belong to the Southern Bush language group.* The numbers of individuals recorded for the various 'tribal' or linguistic groups are presented in Table 1. This information was not available for most of the material examined.

A total of 225 casts of San dentitions (116 males and 109 females) was examined.

The San casts were made at a number of different localities in Botswana. These places are located, for the most part, over the western side of that country (Fig. 2), and they comprised private farms, small settlements dominated by a trading store, and areas around boreholes. Van Reenen (1964) lists some thirteen different places at which San dentitions were examined.

* Thanks to A. Traill (Dept. of Linguistics, University of the Witwatersrand) for these spellings—Editor.

For each individual only a single tooth, usually the left, of any one tooth type (i.e. M_1 , M_2 or M_3) was examined. Thus, throughout, where reference is made to number (N) this refers to both number of teeth and number of indi-

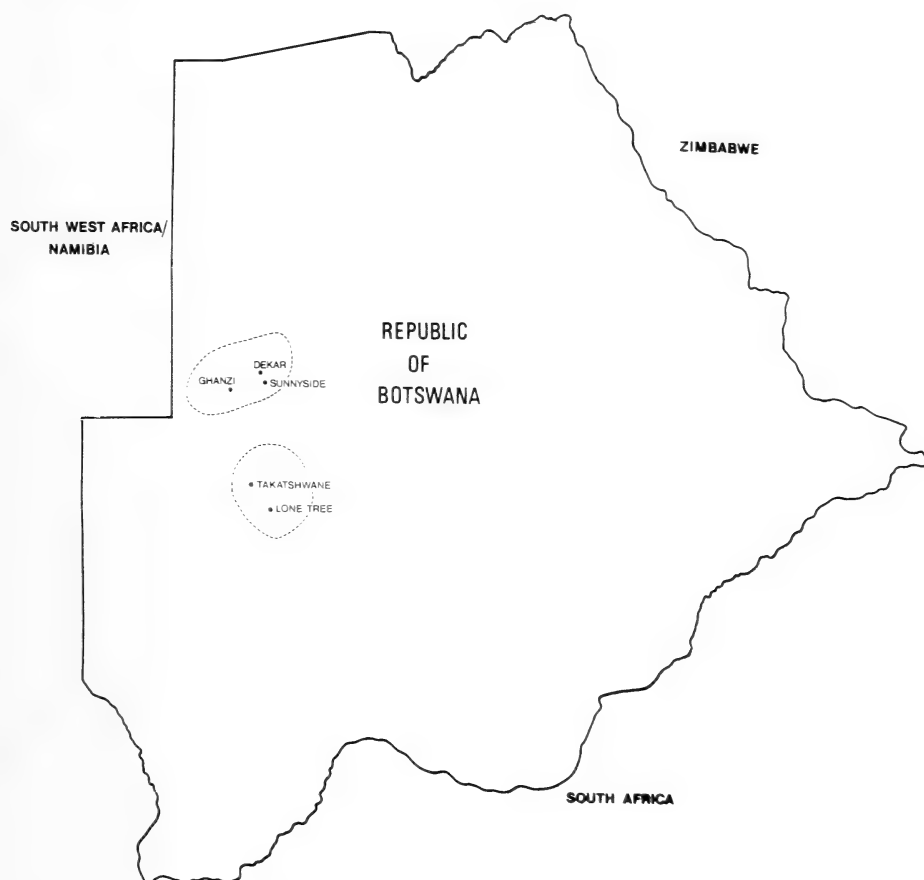


Fig. 2. Areas from which most of the San, whose dental casts were examined, were derived.

viduals. In each instance only those teeth that were undamaged and not obviously diseased were examined. Berry (1976) has shown that most minor dental variants are destroyed by wear, and, therefore, only those teeth that had suffered minimal abrasion or attrition were included. Not every individual examined presented a full dental complement.

Data were recorded on coded sheets and then transferred to computer punch cards. The data were then processed and 'cleaned' via the OSIRIS programs package, and analysed via the SPSS programs package (Nie *et al.* 1975).

DEFINITION AND CLASSIFICATION OF
MORPHOLOGICAL FEATURES

PRINCIPAL CUSP NUMBER

The protoconid, metaconid, hypoconid, entoconid, and hypoconulid are the principal cusps. The criterion accepted here for the presence of a cusp was that it represented a distinct entity, demarcated by deep grooves from adjacent cusps. The number of cusps present were recorded. No attempt was made to quantify the sizes of the cusps. A survey of the literature indicated this mode of notation to be the most widely used; a much smaller number of authors have recorded 'half-sized' cusps (Drennan 1929; Snyder *et al.* 1969; Corruccini 1972), and an even smaller number have utilized either Hrdlička's (1910) or Janzer's (1927) notation schemes for scoring reduced cuspal size (Goldstein 1931; Kiernberger 1955). Neither Hrdlička's nor Janzer's method of counting

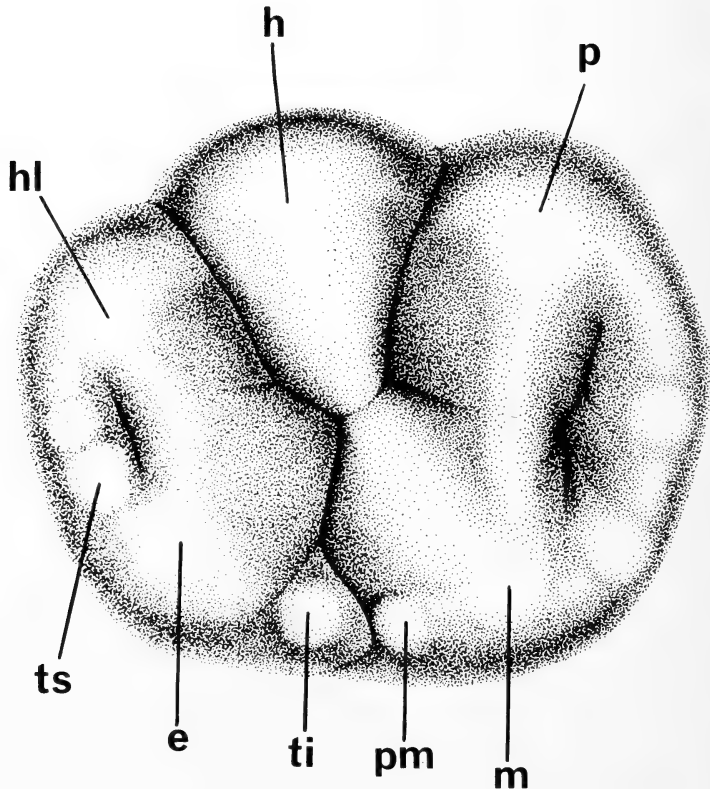


Fig. 3. Drawing of a generalized mandibular left molar showing some of the features examined in this study. e—entoconid, h—hypoconid, hl—hypoconulid, m—metaconid, p—protoconid, pm—postmetaconulid, ti—tuberculum intermedium, ts—tuberculum sextum.

cusps differentiates between the principal cusps and the secondary cusplids (e.g. tuberculum sextum and intermedium). Thus, data presented by authors who followed either of these two systems are not directly comparable with the results of studies in which secondary cusplids have been recorded independently of the principal cusp number.

TUBERCULUM SEXTUM

This is an occasional cusplid situated between the entoconid and the hypoconulid (Fig. 3). Selenka (1898) first proposed the name tuberculum accessorium posteriore internum for such a structure. Hellman (1928) proposed that it be referred to as the C6, and Bennejeant (1936) named it the tuberculum sextum. Matsuda (1961), Turner & Hanihara (1977), Turner & Swindler (1978), and Turner *et al.* (1969) in the literature accompanying their 'Cusp 6' Plaque, have referred to this cusplid as the entoconulid. However, the entoconulid, or pre-entoconulid of MacIntyre (1966) is located on the entocristid, which is mesial of the tip of the entoconid (Van Valen 1966; Szalay 1969; HersHKovitz 1971), whereas the tuberculum sextum is situated distal to the entoconid. Thus, the tuberculum sextum is the homologue of the postentoconulid of the mammalian molar (HersHKovitz 1971).

In some studies the size of this cusplid relative to the size of the hypoconulid has been recorded (e.g. Turner 1970, 1976, 1979; Turner & Hanihara 1977; Turner & Swindler 1978). In the present analysis the absence or presence only of the tuberculum sextum was recorded, and its size gradients were not considered. This feature was regarded as present only if a separate cuspal tip was discernible, bounded by distinct grooves separating it from both the entoconid and hypoconulid. Thus, the tooth classified as category 1 on Turner *et al.* (1969) 'Cusp 6' Plaque would have been regarded here as showing absence of this cusplid.

TUBERCULUM INTERMEDIUM

This occasional cusplid is located between the metaconid and the entoconid (Fig. 3). Selenka (1898) recorded the presence of this feature on some pongid lower molars and proposed the name tuberculum accessorium mediale internum for it. Schwalbe (1916) and Hellman (1928) referred to this structure respectively as the tuberculum intermedium and the C7. These latter two names are the most frequently encountered in the anthropological literature. Robinson (1956), in his description of the South African australopithecine teeth, referred to this tubercle as the lingual or median lingual accessory cusp.

As pointed out by Jorgensen (1956), it is difficult to ascertain whether various authors who have reported data on this cusplid have referred, in all cases, to the same structure. The main reason for this ambiguity appears to be the presence in some teeth of two distinct cusplids between the metaconid

and entoconid. In such teeth the problem is to determine which of these structures is homologous with the tuberculum intermedium.

The cuspid that lies directly distal to the tip of the metaconid (Fig. 3) has been referred to as the metastylid (Osborn 1888; MacIntyre 1966; Van Valen 1966; Szalay 1969), the tuberculum intermedium accessorius antierius (Remane 1960), the postmetaconulid (Herskovitz 1971), and the metaconulid (Turner 1970, 1979; Turner & Hanihara 1977; Turner & Swindler 1978; Turner *et al.* 1970).

The cuspid that is situated directly mesial to the tip of the entoconid has been called the entostylid (Osborn 1888), the tuberculum intermedium accessorium posterius (Remane 1960), the pre-entoconulid (MacIntyre 1966) and the entoconulid (Van Valen 1966; Szalay 1969; Herskovitz 1971).

Selenka (1898), in his description of the tuberculum accessorium mediale intermedium, states that it is usually separated from the metaconid by only a shallow groove, it seldom appears as a part of the entoconid, and that in exceptional cases it shows no continuity with either the metaconid or entoconid. Most workers have stated either explicitly, or indicated in their illustrations of the tuberculum intermedium, that they consider this cuspid to be homologous with the postmetaconulid (Bennejeant 1936; Jorgensen 1956; Robinson 1956; Hanihara 1961; Hanihara & Minamidate 1965; Herskovitz 1971; Matsuda 1961; Turner & Hanihara 1977; Suzuki & Sakai 1956*c*, 1973). However, Turner *et al.* (1970) depict an entoconulid (more precisely a swollen mesial entoconid crest) as a Type 1A development of the tuberculum intermedium in their 'Cusp 7' Plaque.

In a previous study (Grine 1978), a number of teeth were found to possess both a well-defined tuberculum intermedium and a distinct postmetaconulid. In addition, this study revealed a number of molars in which both the mesial crest of the entoconid and the distal aspect of the metaconid were enlarged and separated from the tips of the cusps. Because of this the author cannot subscribe with full confidence to the homology of the tuberculum intermedium with the postmetaconulid.

In the present study the presence of a tuberculum intermedium was recognized only where a distinct cuspid was present between, and well-separated from, both the metaconid and entoconid. Thus, the teeth displayed in Turner *et al.* (1969) 'Cusp 7' Plaque categories 2, 3 and 4 and in Hanihara's (1961) Plaque D9 categories 2 and 3 are recognized as possessing a tuberculum intermedium. No attempt was made to quantify the size of this cuspid.

PRIMARY OCCLUSAL PATTERN

The *Dryopithecus* pattern of the lower molar was first defined and described by Gregory (1916). The concept and diagnosis of this pattern were expanded upon by Gregory (1926*a*, 1934) and Gregory & Hellman (1926*b*). The definition of the pattern eventually included the presence of (i) five principal cusps, (ii) a

symmetrical arrangement of the grooves surrounding the hypoconid forming the tines and the groove between the metaconid and entoconid forming the stem of a Y, and (iii) a broad basal contact of the metaconid and hypoconid.

Gregory (1926a, 1926b) noted that in man the symmetrical arrangement characteristic of the *Dryopithecus* molar has been replaced by a 'cruciform' or '+ pattern' where 'with the crowding forward of the entoconid, the transverse sulcus in front of the entoconid has been brought nearly in line with the transverse sulcus between the protoconid and hypoconid' (1962a: 423).

Gregory & Hellman (1926a, 1926b) added that the metaconid-hypoconid contact of the *Dryopithecus* pattern had been lost in the human molar and had been replaced by a protoconid-entoconid contact, which they considered to be a feature of the 'cruciform' or '+ pattern'.

Hellman (1928) presented a formal scoring scheme and set of definitions by which the occlusal pattern of the lower molar could be classified. He recognized four distinct types: Y5, +5, /4 (or Y4), and +4 (Fig. 4). Reference to Figure 4 indicates that a + pattern was considered by him to possess either a protoconid-entoconid contact (Fig. 4C) or a true cruciform point contact (Fig. 4D). Hellman's (1928) occlusal pattern types were determined according to the arrangement of the lingual and mesiobuccal grooves rather than by the type of cuspal contact exhibited by a tooth. A number of workers have utilized this system of classification.

Weidenreich (1937) considered that the cruciform (true point contact of the metaconid, protoconid, hypoconid and entoconid) and protoconid-entoconid contacts should be regarded as two distinct types. He proposed the

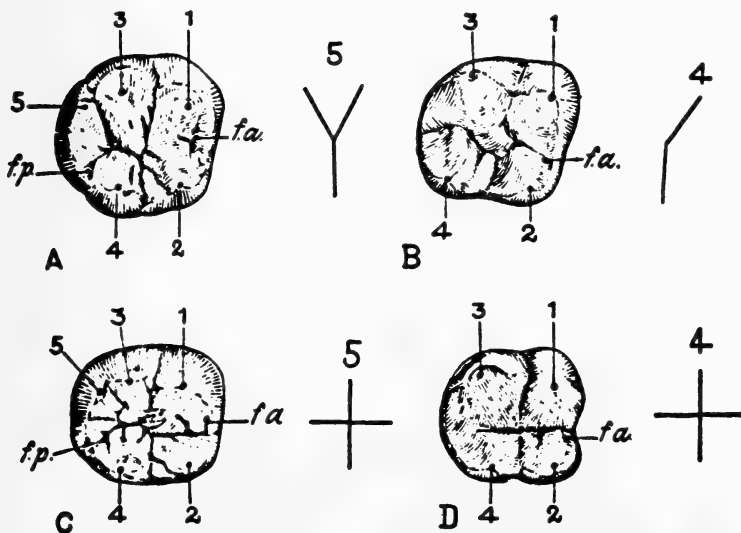


Fig. 4. Left lower molars showing Hellman's criteria for the classification of the primary occlusal pattern (after Hellman 1928: 165, fig. 7).

name 'reversed *Dryopithecus* pattern' for the protoconid-entoconid contact (Weidenreich 1937: 96). However, Weidenreich's suggestion remained unheeded until Senyurek (1952*b*), in a study of the ancient inhabitants of Alaca Höyük, noticed that several lower molars in his sample exhibited a protoconid-entoconid contact. He also regarded this as a significant deviation from both the cruciform and *Dryopithecus* patterns, and he proposed to call this 'deviant plan . . . the protoconid-entoconid connection' (1952*b*: 184). It was not until 1955, though, when Jorgensen described the protoconid-entoconid contact as an 'X pattern', that the differentiation of Hellman's + pattern into two distinct morphological entities became widely accepted by students of human dentition. Jorgensen (1955) recognized three types of lower molar pattern: the Y pattern, characterized by a metaconid-hypoconid contact; the + pattern, defined by a point contact of the protoconid, metaconid, hypoconid and entoconid; and the X pattern (Fig. 5). Thus, whereas Hellman's (1928) scheme employed the

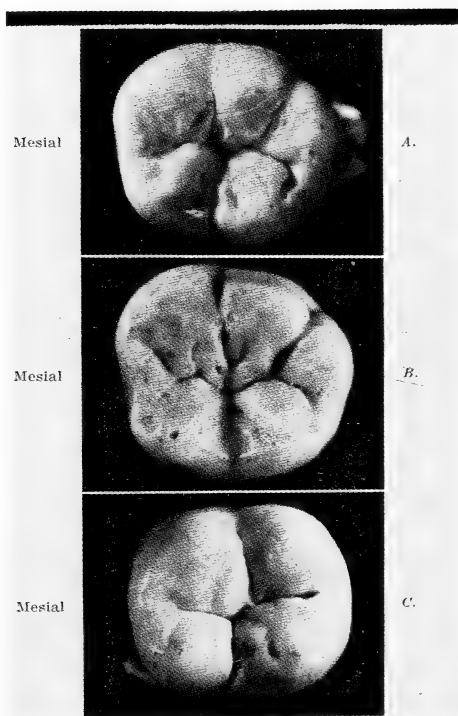


Fig. 5. Right lower molars showing Jorgensen's criteria for the classification of the primary occlusal pattern. A. Y pattern. B. + pattern. C. X pattern. These standards were used in the present study (after Jorgensen 1955: 197, fig. 1).



Fig. 6. Left mandibular third molars showing the H pattern.
A. H pattern with metaconid, protoconid and hypoconid
contacting at a point. B. H pattern with metaconid and hypo-
conid separated by the protoconid.

relationships of the mesiobuccal and lingual grooves, Jorgensen's (1955) molar types were defined on the basis of cuspal contact.

Variants other than Jorgensen's (1955) three categories are encountered. Senyurek (1952a), for example, noted a single molar (M_3) amongst the Chalcolithic and Copper age dentitions from Anatolia in which the protoconid crest was so well developed as to effect contact with the base of the hypoconulid.

The present author has found another interesting variant of cuspal contact in some South African Negro and San lower molars (Grine 1978). In this variant the entoconid is prevented by a grossly enlarged tuberculum intermedium from making contact with either the protoconid or metaconid (Fig. 6). The presence of an enlarged tuberculum intermedium does not necessarily affect the relationships of the protoconid, metaconid and hypoconid, in which case a Y pattern is expressed. However, teeth in which these three cusps contact at a point (Fig. 6A), or in which the metaconid and hypoconid are separated by the protoconid (Fig. 6B), cannot be classified as possessing a conventional + or X pattern. A new category, designated by the letter 'H', was proposed for the classification of crowns exhibiting these latter variants (Grine 1978).

In the present study the cuspal relationships of molars were classified as Y, +, X (Jorgensen 1955), or H. It must be stressed that the Y pattern, as used here, is *not* synonymous with the *Dryopithecus* pattern.

Also, the principal cusp number and the primary occlusal pattern were scored separately. Studies of these two characters have shown them to be unrelated (Jorgensen 1955; Garn *et al.* 1966a, 1966b; Devoto & Cigliano 1970; Devoto *et al.* 1970) or only very slightly related within individual teeth (Rosenzweig & Zilberman 1969).

DEFLECTING WRINKLE

Weidenreich (1937) noted that the dispositions of the crests of the principal cusps may affect the expression of the primary occlusal pattern. He pointed out that on the RM₃ of the Heidelberg (Mauer) mandible while the mesio-buccal and lingual grooves form a straight transverse fissure, 'the metaconid is in contact with the hypoconid by means of a special wrinkle crossing the intersection of the furrows' (Weidenreich 1937: 90). In his description of a LM₃ of *Gigantopithecus blacki*, Weidenreich noted a similar structure where 'the metaconid has a large, well-defined median wrinkle (dw, Plate 10) which emerges from the tip, extends in the direction of the protoconid, and there forms a right angle distally. It transverses the groove between the protoconid and hypoconid and meets the mesial wrinkle of the entoconid approximately in the centre of the occlusal surface . . .' (Weidenreich 1945: 71-72). (Weidenreich's (1945) plate 10 is reproduced here in Figure 7.) He (1945: 84) proposed the name 'deflecting wrinkle' for this structure.

A number of studies have been made of this feature in modern human populations (Hanihara 1956, 1963, 1966, 1970; Hanihara *et al.* 1964, 1975; Suzuki & Sakai 1956b; Morris 1970; Turner 1976, 1979; Turner & Hanihara 1977; Turner & Swindler 1978; Axelsson & Kirveskari 1977). Perhaps even more than any other occlusal feature, the deflecting wrinkle has been subjected to widely disparate schemes of classification.

Hanihara (1961, Plaque D 10) presented a model for the classification of the deflecting wrinkle in which two types were recognized: (i) the central meta-

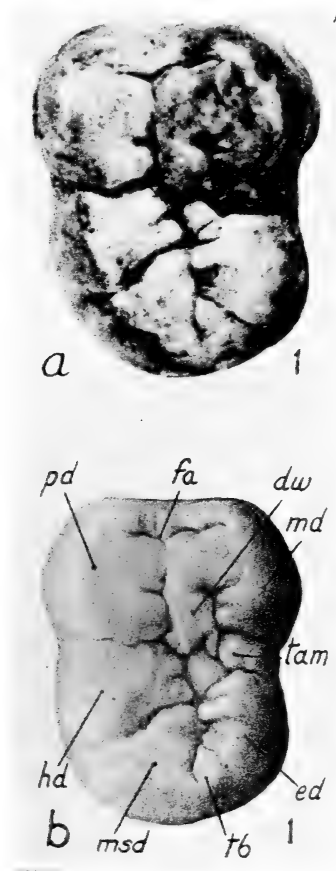


Fig. 7. Left lower molar of *Gigantopithecus blacki* showing the deflected metaconid crest (dw) which Weidenreich named the deflecting wrinkle (after Weidenreich 1945, pl. 10 (fig. b1)).

conid crest was 'very well developed in its thickness' (shown by the dm_2 of his Plaque) and (ii) as shown by the M_1 of his Plaque, the metaconid crest exhibited a true deflecting wrinkle (true in the sense that this feature was defined by Weidenreich). Hanihara (1961: 42) stated that 'the well-developed central ridge seems to be homologous with one which is described as a deflecting wrinkle by Weidenreich'. The crests are, in themselves, homologous, but a straight, well-developed crest is not a deflecting wrinkle. Following Hanihara's mistaken identification of a straight metaconid crest as a deflecting wrinkle, a number of workers (e.g. Hanihara *et al.* 1975; Morris 1970; Turner 1976, 1979; Turner & Swindler 1978; Axelsson & Kirveskari 1977) have either developed or followed classifications in which a thick, straight metaconid ridge is erroneously recognized as a manifestation of a deflecting wrinkle.

An essential feature of the deflecting wrinkle, as defined originally by Weidenreich (1945), is that the metaconid crest courses towards the protoconid and is deflected distally in mid-course. Although Weidenreich described this feature as traversing the longitudinal groove between the hypoconid and entoconid, a deflected crest may be foreshortened so that it does not emerge from between the protoconid and metaconid. Therefore, it is proposed that the deflecting wrinkle be defined as a crest in which the terminal portion, through strong angulation, comes to be orientated along a different axis from the proximal portion. Thus, a deflecting wrinkle may be described as occurring in relation to any of the principal cusps. On this definition a thick, or well-developed, straight cuspal ridge is not recognized as a deflecting wrinkle.

In the present study, the metaconid was examined for evidence of a deflecting wrinkle. The main crest of this cusp was classified as either (i) absent, (ii) straight and weakly developed, (iii) straight and strongly developed, (iv) deflected, or (v) represented by a distinct accessory cuspid.

FOVEA ANTERIOR AND POSTERIOR

The fovea anterior is probably homologous with the trigonid basin (Hrdlička 1924; Weidenreich 1937; Hershkovitz 1971). The name fovea anterior appears to have been proposed by Selenka (1898). Hrdlička (1924) referred to this feature as the precuspidal fossa and Van Valen (1966) proposed to call it the pre-fossid. Elsewhere, the author (Grine 1981*a-d*) has used the names fovea anterior and trigonid basin interchangeably.

In the present study the presence or absence of this fossid was recorded. No distinction of the various configurations assumed by the fovea anterior (Sakura 1979) was made.

The fovea posterior, as named by Selenka (1898) occupies the distal or distolingual corner of the occlusal surface. Hrdlička (1924) referred to this feature as the post-cuspidal basin, but elsewhere in the same paper he used this term in reference to the talonid basin. Van Valen (1966) called this basin the post-fossid, while Hershkovitz (1971) preferred the term post-talonid basin or fossid.

Biggerstaff (1968, 1975) utilized the presence or absence of the fovea posterior in combination with the principal cusp number for classifying the lower molar. He recognized three categories of crowns: (i) four-cusped, (ii) five-cusped without a fovea posterior, and (iii) five-cusped with a fovea posterior. It is not clear why Biggerstaff did not recognize a subdivision of four-cusped teeth, namely with or without a fovea posterior. In the course of the present study a number of four-cusped molars with or without a distal fossid were encountered. Hence, Biggerstaff's (1968, 1975) classification cannot be accepted as complete.

The absence or presence of the fovea posterior was recorded here, and no attempt was made to classify the shape or size of the fossid.

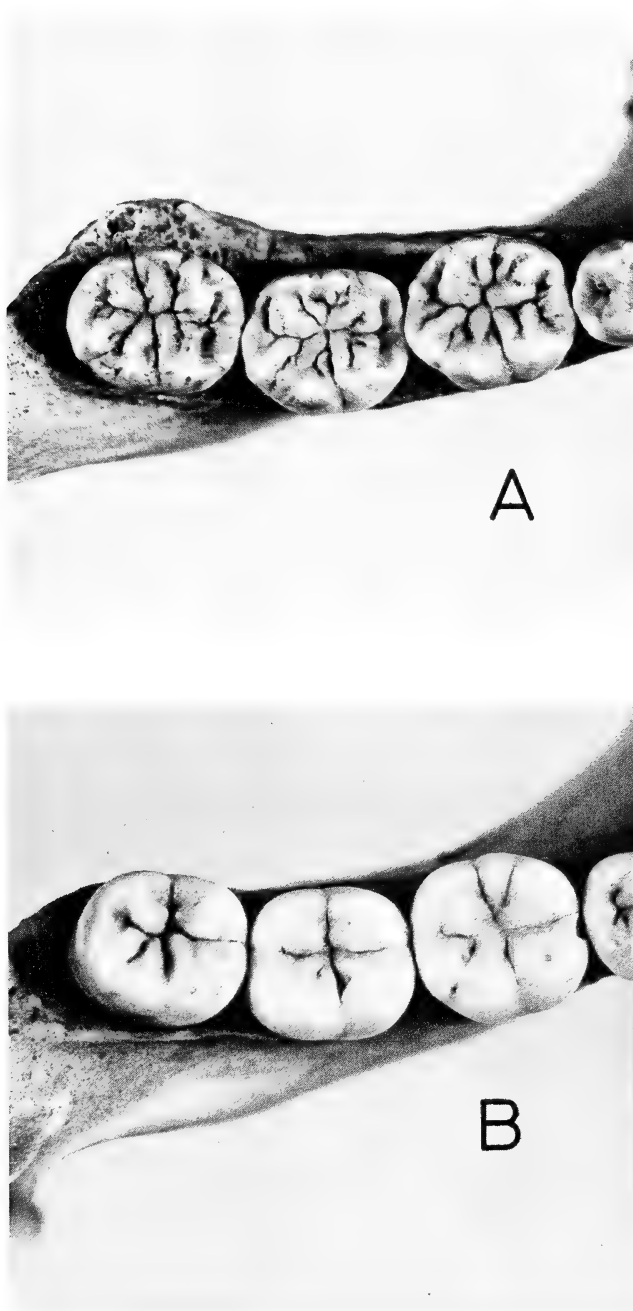


Fig. 8. Lower right permanent molars showing the presence (A) and absence (B) of what was regarded as crenulate enamel in the present study.

ENAMEL WRINKLING

The smoothness or crenulation of occlusal enamel has been considered by relatively few workers in studies of recent human dentitions (Pedersen 1949; Senyurek 1952*b*; Kiernberger 1955; Jacob 1967), although the phylogenetic significance of crenulate enamel was the subject of debate in the earlier literature (e.g. Selenka 1898; De Terra 1905; Gregory 1922; Abel 1931; Adloff 1937, 1938; Weidenreich 1937; Gregory *et al.* 1938).

The paucity of population studies on crenulate enamel is understandable for two reasons: (i) it does not appear possible to classify objectively different degrees of enamel folding, and (ii) enamel wrinkling can be studied only on teeth with either no wear or only minimal wear. Moreover, the genetic factors influencing the expression of these wrinkles are uncertain (Biggerstaff 1968), especially in view of the findings by Ockerse (1943), Malherbe & Ockerse (1944), and Moller (1965, 1967) that cuspal height and relief are inversely proportional to the amount of fluorine intake in humans. These workers found that in areas with relatively high fluorine content in the drinking-water, the teeth of residents exhibited low, smooth cusps and shallow, broad primary grooves.

Pedersen (1949) recorded the presence of wrinkled enamel in the dentition of the east Greenland Eskimo and provided examples of what he regarded as crenulate enamel (Pedersen 1949, plate 14, figs 77–78). The M_3 which Pedersen illustrated in his figure 77 is not regarded as crenulate by the present author, but the M_3 pictured in his figure 78 is considered as such. The difference between crenulate and non-crenulate crowns, as classified here, centres around the degree of development of secondary cuspal crests. Each principal cusp may possess one or more cristids which may be variously represented and delineated. The presence of well-defined secondary cuspal cristids and other subsidiary crests (Fig. 8A) was regarded here as an expression of crenulate enamel.

In the present study the absence or presence of crenulate enamel (Fig. 8) was noted in those molars that had suffered only minimal wear. No attempt was made to classify the different degrees of expression of these accessory cristids.

RESULTS

The frequencies of the principal cusp numbers of the permanent lower molars of the South African Negro and Kalahari San are given in Table 2. No significant sexual differences exist in either racial group in the expression of cusp number on any of the mandibular teeth.

The expression of cusp numbers on the first and third molars of the San and South African Negro are essentially similar. About 99,0 per cent of San and Negro first molars are five-cusped. Approximately 80,0 per cent of San and Negro third molars have five cusps. There is a striking difference between these two populations in the number of cusps on the second molar. Whereas the Negro M_2 shows an almost equal expression of either five or four cusps, the San tooth exhibits five cusps in a high proportion of cases.

TABLE 2

Lower molar cusp number of South African Negro and San.

<i>Population</i>	<i>Sex</i>	<i>Cusp no.</i>	<i>M₁</i>		<i>M₂</i>		<i>M₃</i>	
			<i>N</i>	%	<i>N</i>	%	<i>N</i>	%
Negro	Male	5	242	99,2	136	45,0	236	78,4
		4	2	0,8	166	55,0	61	20,3
		3	—	—	—	—	4	1,3
	Female	5	100	98,0	58	54,7	71	80,7
		4	2	2,0	48	45,3	17	19,3
		3	—	—	—	—	—	—
	Combined	5	342	98,8	194	47,6	307	78,9
		4	4	1,2	214	52,4	78	20,1
		3	—	—	—	—	4	1,0
San	Male	5	62	100,0	42	80,8	30	78,9
		4	—	—	10	19,2	8	21,1
		3	—	—	—	—	—	—
	Female	5	70	98,6	38	76,0	34	82,9
		4	1	1,4	12	24,0	7	17,1
		3	—	—	—	—	—	—
	Combined	5	132	99,2	80	78,4	64	81,0
		4	1	0,8	22	21,6	15	19,0
		3	—	—	—	—	—	—

TABLE 3

Comparison of lower molar cusp numbers of South African Negro and San reported in the literature. Percentage frequencies. Sexes combined.

<i>Population</i>	<i>Tooth</i>	<i>5 cusps</i>	<i>4 cusps</i>	<i>3 cusps</i>	<i>Reference</i>
Negro	<i>M₁</i>	99,2	0,8	—	Jacobson 1967
		98,8	1,2	—	Present study
		55,1	44,9	—	Shaw 1927
	<i>M₂</i>	33,6	66,4	—	Jacobson 1967
		47,6	52,4	—	Present study
		66,4	33,0	0,6	Jacobson 1967
	<i>M₃</i>	78,9	20,1	1,0	Present study
		100,0	—	—	Drennan 1929
		100,0	—	—	Oranje 1934
San	<i>M₁</i>	100,0	—	—	Kiernberger 1955
		100,0	—	—	Van Reenen 1966
		100,0	—	—	Present study
		99,2	0,8	—	Shaw 1927
		25,0	75,0	—	Drennan 1929
	<i>M₂</i>	92,5	7,5	—	Oranje 1934
		100,0	—	—	Kiernberger 1955
		44,4	55,6	—	Van Reenen 1966
		82,4	17,5	—	Present study
		78,4	21,6	—	Drennan 1929
	<i>M₃</i>	86,0	14,0	—	Oranje 1934
		100,0	—	—	Kiernberger 1955
		95,0	5,0	—	Van Reenen 1966
		59,1	40,9	—	Present study
		81,0	19,0	—	Present study

The difference in cuspal number on the M_2 was found to be significant between the Negro and San males ($X^2 = 22,66$; $p < 0,005$), Negro and San females ($X^2 = 6,50$; $p < 0,025$) and between the sexually pooled Negro and San samples ($X^2 = 31,30$; $p < 0,005$).

Shaw (1927) reported frequencies for the cusp number of the San M_2 which are almost exactly the opposite of the frequencies recorded here (Table 3). Oranje (1934) stated that all mandibular molars of the San are characterized by five cusps. Unfortunately, neither Shaw nor Oranje stated the provenance of the specimens that they regarded as San. Drennan (1929) recorded cusp number in the dentition of a supposed San population, the remains of which were exhumed in November 1926 from graves near Colesberg, Cape Province (Table 3). Slome (1929) studied the same skeletal remains and noted that 'these skeletons are the remains of what are supposed to have been Cape Bush people, who died during the smallpox epidemic of 1866. . . . The skeletons from these graves seem to belong to a somewhat mixed group of individuals. Many of them are good Bush types, quite like the Kalahari Bushman . . . a few are Bantu [*sic*] in type and there may be Hottentot types. It is possible that skeleton 29 had some European blood' (Slome 1929: 33-34). Nevertheless, Drennan (1929) included every individual in his 'San' sample. Kiernberger (1955), too, recorded the cusp number for a group of Khoisanoid skulls that had been collected in the Kalahari by Pösch in 1907-1909. Kiernberger (1955) classified the lower molars according to Janzer's (1927) method, and thus she did not record cusp number directly. The cusp numbers of the lower molars in her sample can be determined from her data, however, and these are presented in Table 3. The percentage frequencies presented in Table 3 are not the same as those which Kiernberger (1955: 30) reported in her text, as the figures quoted by her are derived from her total sample, which included a range of people variously recorded as 'Korana, Hottentotten-Buschmannmischlung, Neger-Buschmannmischlung'. Her data also often includes both teeth of any one type from a single individual.

The percentage frequencies of lower molar cusp number recorded here for the Negro and San (Table 2) are comparable with those reported in the more recent surveys of Negro and San dentitions (Table 3), except that there is a disparity between the frequencies reported by Van Reenen (1966) and the present author for cusp number on the San M_3 : the same material was examined by both authors. It is possible that this discrepancy is the result of interobserver differences in counting cusps, but it is also possible that the disparity is the result of the author's recomputation of Van Reenen's (1966) data.

Lower molar cusp numbers in the South African Negro, the Kalahari San and other human populations are presented in Tables 4-6. The human first mandibular molar tends to be five-cusped, and the impression gained from Table 4 is that, despite the disparities sometimes evident in the frequencies recorded for single populations, the incidence of five-cusped first molars in the South African Negro and San is relatively high. The second mandibular tends

TABLE 4

Percentage frequencies of cusp number of lower first permanent molar reported for various human populations. Sexes combined.

Group	Population	5 cusps	4 cusps	Reference
Mongoloid	Amerindian . . .	100,0	—	Brewer-Carias <i>et al.</i> 1976
		95,6	4,4	Perzigian 1976
		73,4	26,6	Campusano <i>et al.</i> 1972
		100,0	—	Dahlberg 1949
		89,0	11,0	Devoto & Cigliana 1970
		90,0	10,0	Devoto & Perrotto 1972
		100,0	—	Goaz & Miller 1966
		99,3	0,6	Goldstein 1948
		80,0	20,0	Hooton 1930
		91,3	8,7	Lavelle 1971
		100,0	—	Leigh 1937
		99,4	0,6	Nelson 1938
		98,5	1,5	Snyder <i>et al.</i> 1969
		95,6	4,5	Goldstein 1931
	Eskimoid . . .	100,0	—	Moorrees 1957
		97,7	1,2	Pedersen 1949
		100,0	—	Hellman 1928
	Chinese . . .	93,2	6,8	Lavelle 1971
	Japanese . . .	91,5	8,5	Matsuda 1961
		98,0	2,0	Suzuki & Sakai 1957
		99,9	0,0	Turner 1979
	Ainu . . .	95,6	4,4	Suzuki & Sakai 1957
		96,8	3,2	Turner 1979
	Hawaiian . . .	98,0	2,0	Chappel 1927
		99,0	1,0	Katich & Turner 1975
	Easter Island . . .	96,0	4,0	Turner & Scott 1976
	Yapese . . .	100,0	—	Harris <i>et al.</i> 1975
Australoid	Austral. Aborigine . . .	97,0	3,0	Campbell 1925
		100,0	—	Hellman 1928
		100,0	—	Lavelle 1971
Melanesian	Naisoi . . .	80,8	19,2	Baillet <i>et al.</i> 1968
	Naisoi & Kwoio . . .	79,0	21,0	Sofaer <i>et al.</i> 1972
	New Britain . . .	96,3	3,7	Dahlberg 1961
		100,0	0,0	Turner & Swindler 1978
Caucasoid	European . . .	82,5	17,5	Berry 1976
		78,2	21,5	Brabant & Twiesselman 1964
		84,5	15,2	Brabant 1971
		89,0	11,0	Hellman 1928
		83,0	17,0	Hellman 1928
		89,4	10,6	Jorgensen 1955
		95,0	5,0	Lavelle 1971
	American . . .	86,0	10,0	Dahlberg 1949
		89,0	11,0	Hellman 1928
		87,0	13,0	Hellman 1928
	Yemeni . . .	85,0	15,0	Rosenzweig & Zilberman 1967
	Cochini . . .	78,0	22,0	Rosenzweig & Zilberman 1967
	Bedouin . . .	83,6	16,4	Rosenzweig & Zilberman 1969
	Samaritans . . .	94,3	5,7	Rosenzweig <i>et al.</i> 1969
	Tristan da Cunha . . .	88,4	11,6	Thomsen 1955
Negroid	Ugandan . . .	99,7	0,2	Barnes 1969
	West African . . .	99,0	1,0	Hellman 1928
		91,7	8,3	Lavelle 1971
		95,1	4,9	Chagula 1960
	East African . . .	98,8	1,2	Present study
	South African . . .	82,0	18,0	Lavelle 1971
	West Indian . . .	99,0	1,0	Hellman 1928
	American Negro . . .	99,2	0,8	Present study
Khoisanoid	San . . .	99,2	0,8	Present study

Note that the rows do not in all cases equal 100 per cent.

TABLE 5

Percentage frequencies of cusp number of lower second permanent molar reported for various human populations. Sexes combined.

Group	Population	5 cusps	4 cusps	3 cusps	Reference
Mongoloid	Amerindian . . .	84,9	15,1		Brewer-Carias <i>et al.</i> 1976
		39,1	60,9		Campusano <i>et al.</i> 1972
		92,4	7,6		Corruccini 1972
		71,0	29,0		Dahlberg 1949
		62,0	?	?	Devoto & Cigliano 1970
		66,6	33,3		Devoto & Perrotto 1972
		72,0	28,0		Goaz & Miller 1966
		27,7	72,3		Goldstein 1948
		32,0	69,0		Hellman 1928
		45,9	54,1		Hooton 1930
		10,1	89,9		Lavelle 1971
		63,0	37,0		Leigh 1937
		32,6	67,4		Nelson 1938
		50,5	49,5		Perzigian 1976
		52,0	48,0		Snyder <i>et al.</i> 1969
		34,9	65,1		Sofaer, Niswander <i>et al.</i> 1972
		45,5	54,5		Sofaer, Niswander <i>et al.</i> 1972
		24,3	75,7		Sofaer, Niswander <i>et al.</i> 1972
		76,8	23,2		Sullivan 1920
		46,0	54,0		Hrdlička 1909
		77,0	20,0		Hrdlička 1909
	Eskimoid . . .	76,6	23,5		Goldstein 1931
		43,0	57,0		Hellman 1928
		55,5	45,5		Moorrees 1957
		60,9	39,1		Pedersen 1949
	Chinese . . .	19,0	81,0		Hellman 1928
		20,4	79,6		Lavelle 1971
	Japanese . . .	28,8	71,2		Matsuda 1961
		68,6	31,4		Turner 1979
	Ainu . . .	42,4	54,2	3,4	Turner & Hanihara 1977
	Hawaiian . . .	21,0	79,0		Chappel 1927
		82,0	18,0		Katich & Turner 1975
	Easter Island . .	47,0	53,0		Turner & Scott 1976
	Yapese . . .	87,0	13,0		Harris <i>et al.</i> 1975
	Polynesia . . .	62,0	38,0		Suzuki & Sakai 1973
Australoid	Austral. Aborigine	37,0	63,0		Campbell 1925
		48,0	52,0		Hellman 1928
		25,0	75,0		Lavelle 1971
		29,2	70,9		Bailit <i>et al.</i> 1968
Melanesian	Naisoi . . .	39,0	61,0		Turner & Swindler 1978
	New Britain . .	13,8	86,2		Dahlberg 1961
	Melanesian . .	28,0	72,0		Sofaer, Maclean <i>et al.</i> 1972
Caucasoid	European . . .	6,9	93,1		Berry 1976
		8,2	83,2	8,3	Brabant 1971
		8,5	91,5		Brabant & Twiesselman 1964
		14,0	86,0		Jorgensen 1955
		7,9	92,1		Lavelle 1971
		1,0	99,0		Hellman 1928
	Yemeni . . .	—	100,0		Rosenzweig & Zilberman 1967
	Cochini . . .	—	100,0		Rosenzweig & Zilberman 1967
	Bedouin . . .	7,0	93,0		Rosenzweig & Zilberman 1969
	Samaritans . .	5,8	94,2		Rosenzweig <i>et al.</i> 1969
	Tristan da Cunha	1,3	98,7		Thomsen 1955
	Egyptian . . .	5,0	95,0		Leigh 1934
	Indian . . .	16,6	83,4		Sullivan 1920
Negroid	Ugandan . . .	24,1	75,9		Barnes 1969
	West African . .	25,0	75,0		Hellman 1928
		25,0	75,0		Lavelle 1971
	East African . .	18,6	81,4		Chagula 1960
	South African .	47,6	52,4	0,0	Present study
	West Indian . .	24,4	75,6		Lavelle 1971
	American Negro .	30,0	70,0		Hellman 1928
Khoisanoid	San . . .	78,4	21,6	0,0	Present study

Note that the rows do not in all cases equal 100 per cent.

TABLE 6

Percentage frequencies of cusp number of lower third permanent molar reported for various human populations. Sexes combined.

Group	Population	5 cusps	4 cusps	3 cusps	Reference
Mongoloid	Amerindian . . .	80,1	19,5		Corruccini 1972
		80,0	?	?	Devoto & Cigliano 1970
		83,3	16,6		Devoto & Perrotto 1972
		62,1	37,9		Goaz & Miller 1966
		51,0	49,0		Leigh 1937
		59,4	40,6		Nelson 1938
		72,6	27,4		Perzigian 1976
		38,5	61,5		Hooton 1930
		75,0	24,0		Hellman 1928
		99,3	0,6		Goldstein 1948
		58,0	42,0		Lavelle 1971
	Eskimoid . . .	75,0	25,0		Moorrees 1957
		88,9	11,1		Pedersen 1949
		52,0	48,0		Hellman 1928
		89,9	10,2		Goldstein 1948
	Chinese . . .	42,0	58,0		Lavelle 1971
		50,0	50,0		Hellman 1928
	Japanese . . .	87,5	12,5		Turner 1979
	Ainu . . .	64,7	35,3		Turner & Hanihara 1977
	Hawaiian . . .	86,0	14,0		Chappel 1927
		67,0	33,0		Katich & Turner 1975
	Easter Island . . .	80,0	20,0		Turner & Scott 1976
	Yapese . . .	100,0	0,0		Harris <i>et al.</i> 1975
Australoid	Austral. Aborigine	73,0	27,0		Campbell 1925
		86,0	14,0		Hellman 1928
		63,6	36,4		Lavelle 1971
Melanesian	Naisoi . . .	58,0	42,0		Bailit <i>et al.</i> 1968
	New Britain . . .	80,0	20,0		Dahlberg 1961
		84,4	15,6		Turner & Swindler 1978
Caucasoid	European . . .	60,0	39,8		Brabant 1971
		52,0	47,0	0,9	Brabant & Twiesselman 1964
		60,6	39,4		Jorgensen 1955
		35,7	64,3		Lavelle 1971
	American . . .	38,0	62,0		Hellman 1928
	Tristan da Cunha	71,4	28,5		Thomsen 1955
	Egyptian . . .	37,0	57,0	?	Leigh 1934
Negroid	Ugandan . . .	60,0	40,0		Barnes 1969
	West African . . .	79,0	20,0		Hellman 1928
		61,1	38,9		Lavelle 1971
		58,9	40,7	0,4	Chagula 1960
	South African . . .	78,9	20,1	1,0	Present study
	West Indian . . .	63,6	36,4		Lavelle 1971
	American Negro . . .	67,0	33,0		Hellman 1928
Khoisanoid	San . . .	81,0	19,0	0,0	Present study

Note that the rows do not in all cases equal 100 per cent.

to be four-cusped (Table 5), and here, too, the incidences of five-cusped second molars in the South African Negro and San are relatively high. The third molar tends to be five cusped in recent human populations, and once again the incidences of five-cusped third molars in the South African Negro and Kalahari

San appear to be relatively high (Table 6) by comparison with other human populations.

The frequencies of the various occlusal patterns on the permanent lower molars of the South African Negro and Kalahari San are presented in Table 7. Chi-square analyses revealed that no significant sexual differences exist in either population group in the expression of the primary occlusal pattern on any of the lower molar types. In the Negro the female tends to have a Y pattern (i.e. a metaconid-hypoconid contact) more often than the male on all molars. The San female tends to evince a Y pattern on the M_1 somewhat more often than the male, while the frequencies of this pattern on the second and third molars are slightly higher in the San male.

The expression of cuspal contact patterns on the first and third molars of the San and Negro are essentially similar. The San tends to possess a Y pattern more often on the M_1 and the Negro shows a slightly higher frequency of the + pattern on the M_1 and X pattern on the M_3 . The interracial differences in occlusal pattern configuration on the first and third molars are not statistically significant. However, the difference in primary occlusal pattern expression on the M_2 was found to be statistically significant between Negro and San males ($X^2 = 22,82$; $p < 0,005$), Negro and San females ($X^2 = 6,68$; $p < 0,01$ with X and Y pattern cells only), and between the sexually pooled San and

TABLE 7
Lower molar primary occlusal patterns of South African Negro and San.

Population	Sex	Cusp pattern	M_1		M_2		M_3	
			N	%	N	%	N	%
Negro	Male . . .	Y	195	79,9	68	22,5	40	13,3
		+	44	18,0	205	67,9	112	37,3
		X	5	2,0	29	9,6	138	46,0
		H	—	—	—	—	10	3,3
	Female . . .	Y	82	83,7	29	27,4	12	14,0
		+	13	13,3	70	66,6	37	43,0
		X	3	3,1	7	6,6	34	39,5
		H	—	—	—	—	3	3,5
	Combined . .	Y	277	81,0	97	23,8	52	13,5
		+	57	16,7	275	67,4	149	38,6
		X	8	2,3	36	8,8	172	44,6
		H	—	—	—	—	13	3,4
San	Male . . .	Y	52	83,9	27	51,9	9	23,7
		+	10	16,1	24	46,2	14	36,8
		X	—	—	1	1,9	14	36,8
		H	—	—	—	—	1	2,6
	Female . . .	Y	66	93,0	25	50,0	7	17,1
		+	5	7,0	24	48,0	17	41,5
		X	—	—	1	2,0	15	36,6
		H	—	—	—	—	2	4,9
	Combined . .	Y	118	88,7	52	51,0	16	20,2
		+	15	11,3	48	47,0	31	39,2
		X	—	—	2	2,0	29	36,7
		H	—	—	—	—	3	3,8

Negro samples ($X^2 = 31,16$; $p < 0,005$). The San possesses a Y pattern on the second molar in a significantly higher percentage of cases than the Negro, while the Negro molar more often shows a cruciform (+) type of cuspal contact (Table 7). There is also a striking difference between these two racial groups in the number of cusps on this molar.

In both the San and the Negro the first molars show the highest frequencies of the Y pattern with the second and third molars showing progressively lower frequencies of this pattern. The second molars of both populations show an increased frequency in the + pattern over the first molars, while the third molars evince a X pattern more often than the second (or first) molars.

The H pattern was encountered only on the third molars of both populations. The frequency of expression of this variant pattern is low and almost identical in the San (3,8 per cent) and the Negro (3,4 per cent).

Van Reenen (1966) and Jacobson (1967) have reported data on the frequencies of the primary occlusal pattern in San and South African Negro populations respectively. Although neither stated the scheme by which they classified the occlusal pattern, it is apparent from Jacobson's illustrations and, since they recognized only the Y and + patterns, that Hellman's (1928) standard was employed by both. The frequencies reported by them are compared with the incidences of Y and + (where + consists of combined + and X pattern frequencies) recorded in the present study in Table 8. Both Van Reenen (1966) and Jacobson (1967) recorded higher frequencies of the Y pattern on the M_1 , and lower frequencies of this pattern on the M_2 and M_3 for the San and Negro than the frequencies reported here. In no instance, however, are the incidences reported by Van Reenen (1966), Jacobson (1967), and the present author markedly different.

TABLE 8

Percentage incidence of primary occlusal patterns of lower permanent molars recorded for Negroid and Khoisanoid populations. Sexes combined.

Population	M_1		M_2		M_3		Reference
	Y	+	Y	+	Y	+	
Ugandan*	83,8	16,2	32,5	67,5	19,2	80,8	Barnes 1969
East African	86,9	13,1	20,2	79,8	20,3	79,7	Chagula 1960
West African	100,0	—	29,0	71,0	23,0	76,0	Hellman 1928
	86,1	13,9	25,0	75,0	30,6	69,4	Lavelle 1971
South African	89,8	10,2	12,3	87,7	7,7	92,6	Jacobson 1967
*	81,0	19,0	23,8	76,2	13,5	86,5	Present study
American	99,0	1,0	27,0	73,0	7,0	93,0	Hellman 1928
West Indian	83,6	16,4	30,0	70,0	32,4	67,6	Lavelle 1971
Kalahari San	98,1	1,9	32,5	67,5	13,6	86,4	Van Reenen 1966
*	88,7	11,3	51,0	49,0	20,2	79,8	Present study

*Frequencies of + pattern obtained by combining data for + and X patterns for comparison.

Comparison of the data for the South African Negro and San with various Negro populations (Table 8) indicates that the first and third molars of both the San and South African Negro and the second molars of the South African

Negro are similar to other Negro populations in the relative frequency of occlusal pattern expression. The M_2 of the San, according to the present data, tends to have a Y pattern more often than do any of the Negro populations. According to Van Reenen's (1966) results, the frequency of the Y pattern on the M_2 of the San is higher than in all other Negro populations except the Teso of Uganda (Barnes 1969).

Kiernberger (1955) examined the occlusal surface pattern of the Khoisanoid lower molar, but she utilized Janzer's (1927) method of classification. Janzer (1927) recognized three different occlusal types, the foundation of each being cusp number and occlusal outline. Although Kiernberger (1955: 25) states that 'in die dritte Gruppe der unteren . . . Molaren gehören diejenigen,

TABLE 9

Percentage frequencies of primary occlusal patterns of lower first permanent molar reported for various human populations. Sexes combined. These authors have followed Hellman's (1928) method.

Group	Population	Y	+	Reference
Mongoloid	Amerindian	73,4	26,6	Campusano <i>et al.</i> 1972
		100,0	—	Hellman 1928
		63,0	37,0	Corruccini 1972
		99,4	0,6	Dahlberg 1949
		69,3	30,6	Goldstein 1948
		88,4	11,6	Lavelle 1971
		88,6	11,4	Nelson 1938
		84,0	16,0	Snyder <i>et al.</i> 1969
	Eskimoid	91,1	9,0	Goldstein 1948
		97,0	3,0	Hellman 1928
		41,4	58,6	Moorrees 1957
		94,7	4,1	Pedersen 1949
	Chinese	92,4	7,6	Lavelle 1971
		100,0	—	Hellman 1928
Australoid	Austral. Aborigine . .	100,0	—	Hellman 1928
		97,7	2,3	Lavelle 1971
Melanesian	Melanesian	96,8	3,2	Dahlberg 1961
		60,1	39,8	Lombardi 1975
Caucasoid	European —	46,0	53,7	Brabant 1971
		85,0	15,0	Brabant & Twiesselmann 1964
		79,0	21,0	Lavelle 1971
	American	92,0	4,0	Dahlberg 1949
		94,0	6,0	Hellman 1928
		53,0	47,0	Rosenzweig & Zilberman 1967
	Cochini	57,0	43,0	Rosenzweig & Zilberman 1967
	Bedouin	70,4	29,6	Rosenzweig & Zilberman 1969
	Samaritans	87,1	12,9	Rosenzweig <i>et al.</i> 1969
	Tristan da Cunha . .	74,7	25,2	Thomsen 1955
Negroid	East Africa	86,9	13,1	Chagula 1960
	West Africa	100,0	—	Hellman 1928
		86,1	13,9	Lavelle 1971
	South Africa	89,8	10,2	Jacobson 1967
	American Negro . . .	99,0	1,0	Hellman 1928
	West Indian	83,6	16,4	Lavelle 1971
Khoisanoid	San	98,1	1,9	Van Reenen 1966

Note that the rows do not in all cases equal 100 per cent.

TABLE 10

Percentage frequencies of primary occlusal patterns of lower first permanent molar reported for various human populations. Sexes combined. These authors have followed Jorgensen's (1955) method.

Group	Population	Y	+	X	Reference
Mongoloid	Amerindian . . .	51,6	29,4	19,0	Brewer-Carias <i>et al.</i> 1976
		65,0	35,0	0,0	Devoto & Cigliano 1970
		69,2	23,1	7,7	Goaz & Miller 1966
	Chinese	?	14,2	?	Sofaer <i>et al.</i> 1972
		?	?	4,1	Turner 1976
		71,3	22,9	5,8	Matsuda 1961
	Japanese	?	?	6,6	Turner 1976
		70,7	22,7	6,7	Suzuki & Sakai 1957
		?	?	3,2	Turner 1976
	Ainu	88,9	7,9	3,2	Turner 1979
		93,4	3,3	3,3	Turner & Hanihara 1977
		56,5	34,8	8,7	Suzuki & Sakai 1957
	Polynesian	82,4	12,3	5,3	Suzuki & Sakai 1973
		85,0	?	?	Turner & Scott 1976
		89,0	?	?	Katich & Turner 1975
	Hawaiian	73,0	?	?	Harris <i>et al.</i> 1975
	Yapese	?	33,0	?	Sofaer <i>et al.</i> 1972
Melanesian	Melanesian	54,9	45,1	0,0	Bailit <i>et al.</i> 1968
	Naisoi	92,7	7,3	0,0	Turner & Swindler 1978
	New Britain	55,5	34,6	9,9	Berry 1976
Caucasoid	European	69,2	13,7	17,1	Jorgensen 1955
		69,2	18,1	12,7	Jorgensen 1955
		29,8	59,7	10,5	Takehisa 1957
Negroid	American	83,8	16,2	—	Barnes 1969
	Ugandan	81,0	16,7	2,3	Present study
Khoisanoid	South Africa	88,7	11,3	0,0	Present study

die vier Höcker besitzen und deren Furchen Kreuzförmig angeordnet sind', the alignment of the mesiobuccal and lingual grooves, rather than cuspal contact, appears to be the basis for the cruciform (Kreuzförmig) pattern. Thus, Kiernberger's data on the occlusal morphology of the Khoisanoid lower molar do not seem to be comparable with the primary occlusal pattern data recorded here.

The majority of authors who have reported frequencies of primary occlusal patterns for different human populations have utilized either Hellman's (1928) or Jorgensen's (1955) methods of classification. As pointed out above, these two systems are not directly comparable in all instances as Hellman's + type includes both the + and X patterns of Jorgensen. The data presented by various authors for different populations are tabulated in Tables 9–14, according to the classificatory method employed by each author. Several workers have created and/or utilized methods of classification that are either slight modifications of, or completely different from, either the Hellman or Jorgensen systems. It is essential that these various classifications be recognized as distinct when one attempts to compare data on different population groups recorded by various authors. Numerous workers have, nevertheless, compiled rather extensive

tables of reported occlusal pattern frequencies in which the incomparability of much of the reported data has been ignored (e.g. one list included studies that had used variously Hellman's (1928), Jorgensen's (1955), and Steslicka's (1948) categories).

Tables 9-14 indicate that the human first permanent molar tends usually to have a Y pattern, while the second and third molars evince the + or X pattern more frequently than the Y. In those studies that considered the X pattern, the M_3 possesses the highest frequency, the M_2 a somewhat lower, and the M_1 the lowest frequency of this pattern (Tables 10, 12, 14). It is evident also that, in general, the expression of the primary occlusal pattern is more variable than the principal cusp number for each molar type.

Examination of Tables 9-14 indicates that, while there is a considerable degree of intragroup variability in the frequencies of expression reported

TABLE 11

Percentage frequencies of primary occlusal patterns of lower second permanent molar reported for various human populations. Sexes combined. These authors have followed Hellman's (1928) method.

Group	Population	Y	+	Reference
Mongoloid	Amerindian	39,1	60,9	Campusano <i>et al.</i> 1972
		4,5	95,5	Corruccini 1972
		3,0	97,0	Dahlberg 1949
		4,9	95,1	Goldstein 1948
		1,0	99,0	Hellman 1928
		5,8	94,2	Lavelle 1971
		9,6	90,4	Nelson 1938
		38,5	61,5	Snyder <i>et al.</i> 1969
	Eskimoid	15,8	84,3	Goldstein 1948
		13,0	87,0	Hellman 1928
		0,0	100,0	Moorrees 1957
	Chinese	24,3	76,6	Pedersen 1949
		0,0	100,0	Hellman 1928
		15,6	84,4	Lavelle 1971
Australoid	Austral. Aborigine . .	5,0	95,0	Hellman 1928
		22,7	77,3	Lavelle 1971
Melanesian	Melanesian	12,8	87,2	Dahlberg 1961
Caucasoid	European	33,1	66,6	Brabant 1971
		9,5	90,5	Brabant & Twiesselman 1964
		7,1	92,9	Lavelle 1971
	American	5,0	95,0	Hellman 1928
	Yemeni	9,0	91,0	Rosenzweig & Zilberman 1967
	Cochini	5,0	95,0	Rosenzweig & Zilberman 1969
	Bedouin	7,0	93,0	Rosenzweig & Zilberman 1969
	Samaritan	12,6	87,4	Rosenzweig <i>et al.</i> 1969
	Tristan da Cunha . .	7,9	92,1	Thomsen 1955
Negroid	East African	20,2	79,8	Chagula 1960
	West African	29,0	71,0	Hellman 1928
		25,0	75,0	Lavelle 1971
	South African	12,3	87,7	Jacobson 1967
	American	27,0	73,0	Hellman 1928
	West Indian	30,0	70,0	Lavelle 1971
Khoisanoid	San	32,5	67,5	Van Reenen 1966

TABLE 12

Percentage frequencies of primary occlusal patterns of lower second permanent molar reported for various human populations. Sexes combined. These authors have followed Jorgensen's (1955) method.

Group	Population	Y	+	X	Reference
Mongoloid	Amerindian . . .	5,6	34,8	59,6	Brewer-Carias <i>et al.</i> 1976
		—	45,0	55,0	Devoto & Cigliano 1970
		10,7	53,3	36,0	Goaz & Miller 1966
	Japanese . . .	4,2	41,0	54,7	Matsuda 1961
		4,5	44,2	51,3	Suzuki & Sakai 1956a
		31,5	28,8	39,7	Turner 1979
	Ainu . . .	11,3	32,1	56,6	Turner & Hanihara 1977
	Polynesian . . .	11,0	?	?	Turner & Scott 1976
		10,1	38,0	51,9	Suzuki & Sakai 1973
	Hawaiian . . .	20,0	?	?	Katich & Turner 1975
Melanesian	Naisoi . . .	13,1	86,9	—	Bailit <i>et al.</i> 1968
	New Britain . . .	8,1	67,6	24,3	Turner & Swindler 1978
	Melanesian . . .	?	80,0	?	Sofaer, Maclean <i>et al.</i>
					1972
Caucasoid	European . . .	14,9	54,6	30,5	Berry 1976
		16,7	26,8	56,6	Jorgensen 1955
		14,3	27,2	58,5	Jorgensen 1955
	American . . .	—	42,1	57,9	Takehisa 1957
Negroid	Ugandan . . .	32,5	60,0	7,5	Barnes 1969
	South African . . .	23,8	67,4	8,8	Present study
Khoisanoid	San . . .	51,0	47,0	2,0	Present study

(e.g. frequencies for the Y pattern on the M_1 of Mongoloid peoples range between 41,4–100,0 per cent), overall the Australoid peoples tend to possess the highest frequencies of Y-patterned first molars followed closely by the San and the Negro. The Caucasoid populations that have been examined tend to show the lowest frequencies of the Y pattern on the M_1 . Conversely, the Caucasoid populations tend to display the highest frequencies of + patterns and/or X patterns on the first mandibular molars.

The percentage frequencies of Y patterns on second molars that have been recorded for various human populations range from total absence to 51,0 per cent (Tables 11–12). Van Reenen (1966) recorded that 32,5 per cent of San M_2 's possess a Y pattern, while the present author found 51,0 per cent of these molars to be Y patterned. The latter figure represents the highest incidence recorded for any human population, and Van Reenen's figure is amongst the highest of recorded frequencies (Tables 11–12). It appears, therefore, that the Y pattern is shown more frequently on the M_2 of the San than on this tooth in most other human populations. Whereas the Melanesian and Australoid peoples tend to possess the highest frequencies of Y-patterned first molars, the second molars of the populations appear to show relatively low frequencies of Y pattern expression. There seems to be little difference in the incidence of Y pattern expression on the M_2 amongst the Mongoloid, Australoid, Caucasoid, and Negroid populations (Tables 11–12).

Whereas the San tends to have the Y pattern relatively frequently on the M_1 and M_2 , the incidences of this pattern on the M_3 as reported by both Van Reenen (1966) and the present author are amongst the lower recorded for other human populations (Tables 13–14). The frequencies of Y-patterned M_3 's in the South African Negro recorded by both Jacobson (1967) and the author are the lowest recorded for any other Negroid population with the exception of the American Negro (Tables 13–14). The frequencies of Y-patterned third molars in the Melanesian and Australoid populations are amongst the lower percentage incidences recorded for recent human populations.

However, comparison of only that data recorded by authors who used Jorgensen's (1955) method of crown classification (Table 14) indicates that the San M_3 shows a Y pattern more frequently than in any other population (the Teso of Uganda and the Ainu show comparable frequencies though), and that the frequency of X-patterned M_3 's in this population is one of the lowest recorded to date.

Chi-square evaluation of cuspal number and primary occlusal patterns on the lower molars of the South African Negro and San revealed that the two are dependent variables only on the M_2 of the Negro male ($X^2 = 6,47$; $p = 0,04$)

TABLE 13

Percentage frequencies of primary occlusal patterns of lower third permanent molar reported for various human populations. Sexes Combined. These authors have followed Hellman's (1928) method.

Group	Population	Y	+	Reference
Mongoloid	Amerindian	7,7	92,3	Corruccini 1972
		29,0	71,0	Dahlberg 1949
		18,7	81,4	Goldstein 1948
		5,0	94,0	Hellman 1928
		18,8	78,2	Lavelle 1971
		13,2	86,8	Nelson 1938
	Eskimoid	20,4	79,7	Goldstein 1948
		—	100,0	Hellman 1928
		—	100,0	Moorrees 1957
	Chinese	23,8	76,2	Pedersen 1949
		—	100,0	Hellman 1928
		43,4	56,6	Lavelle 1971
Australoid	Austral. Aborigine . .	14,0	86,0	Hellman 1928
		18,2	81,8	Lavelle 1971
Melanesian	Melanesian	16,6	83,4	Dahlberg 1961
Caucasoid	European	43,4	56,4	Brabant 1971
		30,4	69,5	Brabant & Twiesselman 1964
		6,8	93,2	Lavelle 1971
	American	4,0	96,0	Hellman 1928
	Tristan da Cunha . .	71,4	28,5	Thomsen 1955
Negroid	East African	20,3	79,7	Chagula 1960
	West African	23,0	76,0	Hellman 1928
		30,6	69,4	Lavelle 1971
	South African	7,4	92,6	Jacobson 1967
	American	7,0	93,0	Hellman 1928
Khoisanoid	West Indian	32,4	67,6	Lavelle 1971
	San	13,6	86,4	Van Reenen 1966

TABLE 14

Percentage frequencies of primary occlusal patterns of lower third permanent molar reported for various human populations. Sexes combined. These authors have followed Jorgensen's (1955) method.

Group	Population	Y	+	X	References
Mongoloid	Amerindian . . .	6,9	48,2	44,8	Goaz & Miller 1966
		0,0	0,0	100,0	Devoto & Perrotto 1972
	Japanese . . .	11,8	13,7	74,5	Turner 1979
Melanesian	Ainu . . .	17,1	5,7	77,1	Turner & Hanihara 1977
	Naisoi . . .	7,1	81,0	11,9	Bailit <i>et al.</i> 1968
	New Britain . . .	0,0	22,2	77,8	Turner & Swindler 1978
Caucasoid	European . . .	10,9	12,2	76,9	Jorgensen 1955
		11,2	17,5	71,3	Jorgensen 1955
Negroid	Ugandan . . .	19,2	46,1	34,3	Barnes 1969
	South African . . .	13,5	38,6	44,6	Present study
Khoisanoid	San . . .	20,2	39,2	36,7	Present study

and on the M_1 of the Negro female ($X^2 = 15,24$; $p = 0,005$). No evidence of variable dependence was found for any of the other Negro molars, nor were cusp number and occlusal pattern found to be dependent in any case in the San. Studies of these two features on the lower molars of other human populations have also found them to be unrelated (Jorgensen 1955; Garn *et al.* 1966*a*, 1966*b*; Devoto & Cigliano 1970; Devoto *et al.* 1970) or only very slightly related within individuals (Rosenzweig & Zilberman 1969).

Nevertheless, numerous workers have recorded the cusp number and occlusal pattern together (e.g. Y5, Y4, +5, +4, etc.). In order to facilitate comparisons with the results presented in such studies, the frequencies of cusp number-occlusal pattern 'complements' on the South African Negro and San lower molars are presented in Table 15.

The first molars of both the Negro male and female most frequently evince a Y5 pattern. This is true also of the San first molar. The third molars of both the Negro and San males show an X5 pattern most frequently, while the third molars of the Negro and San females exhibit most commonly a +5 pattern. However, in the sexually pooled samples the Negro M_3 is found to display most frequently an X5 pattern (because of the larger sample of male molars) but the San M_3 is found to evince a +5 pattern most often.

Both the Negro male and female show a +4 pattern most frequently on the second molar (Table 15). The San male has a Y5 pattern most commonly, but this frequency is only slightly higher than that for the +5 pattern. The Y5 and +5 patterns occur with the same frequency on the second molars of the San female, and both these patterns are more common than any other. In the sexually pooled San sample the Y5 pattern is found most frequently on the second molar, with the +5 pattern encountered in only a slightly lower percentage of cases.

The incidences of metaconid deflecting wrinkles (as this feature is here defined) on the lower molars of the South African Negro and San are presented in Table 16.

TABLE 15
Lower molar cusp number and cuspal pattern of the South African Negro and Kalahari San.

Sex	Cusp pattern	Cusp no.	South African Negro			Kalahari San		
			M_1 N	M_2 N	M_3 N	M_1 N	M_2 N	M_3 N
Male	.	5	194 79,5	34 11,3	31 10,3	52 83,9	22 42,3	8 21,1
	.	4	1 0,4	36 12,0	9 3,0	—	5 9,6	1 2,6
	.	5	44 18,0	81 26,9	83 27,7	10 16,1	20 38,5	10 26,3
	+	4	—	121 40,2	28 9,3	—	4 7,7	4 10,5
	X	5	5 2,0	18 6,0	116 38,7	—	—	11 29,0
Female	X	4	—	11 3,7	23 7,7	—	—	3 7,9
	X	4	—	—	10 3,3	—	1 1,9	1 2,6
	H	5	—	—	9 10,5	—	—	6 14,6
	Y	5	81 82,7	20 19,0	9 3,5	65 91,5	19 38,0	6 14,6
	Y	4	1 1,0	9 8,6	3 3,5	1 1,4	6 12,0	1 2,4
Combined	+	5	13 13,3	34 32,4	30 34,9	5 7,0	19 38,0	15 36,6
	+	4	—	35 33,3	7 8,1	—	5 10,0	2 4,9
	X	5	2 2,0	3 2,9	28 32,6	—	—	12 29,3
	X	4	1 1,0	4 3,8	6 7,0	—	1 2,0	3 7,3
	H	5	—	—	3 3,5	—	—	2 4,9
Combined	.	5	275 80,4	54 13,3	40 10,4	117 88,0	41 40,2	14 17,7
	.	4	2 0,6	45 11,1	12 3,1	1 0,8	11 10,8	2 2,5
	+	5	57 16,7	115 28,3	113 29,3	15 11,3	39 38,2	25 31,6
	+	4	—	156 38,4	35 9,1	—	9 8,8	6 7,6
	X	5	7 2,0	21 5,2	114 37,3	—	—	23 29,1
Combined	X	4	1 0,3	15 3,7	29 7,5	—	—	6 7,6
	X	4	—	—	13 3,4	—	2 2,0	3 3,8
	H	5	—	—	—	—	—	—

TABLE 16

Metaconid crest morphology of lower permanent molars of the South African Negro and Kalahari San.

Population and sex		Tooth	Absent		Weak		Strong		Deflected		Cuspid	
			N	%	N	%	N	%	N	%	N	%
Negro												
Male . . .	M ₁	15	6,3	73	30,7	112	47,1	38	15,9	0	0,0	
	M ₂	120	41,2	151	51,9	14	4,8	6	2,1	0	0,0	
	M ₃	122	41,8	143	49,0	14	4,8	12	4,1	1	0,3	
Female . . .	M ₁	2	2,0	15	15,2	56	56,6	26	26,3	0	0,0	
	M ₂	41	39,4	55	52,9	8	7,7	0	0,0	0	0,0	
	M ₃	37	42,0	43	48,9	3	3,4	5	5,7	0	0,0	
Combined . . .	M ₁	17	5,0	88	26,1	168	49,9	64	19,0	0	0,0	
	M ₂	161	40,8	206	52,2	22	5,6	6	1,5	0	0,0	
	M ₃	159	41,8	186	49,0	17	4,5	17	4,4	1	0,3	
San												
Male . . .	M ₁	0	0,0	13	21,0	36	58,1	13	20,9	0	0,0	
	M ₂	2	3,9	39	76,5	8	15,7	2	3,9	0	0,0	
	M ₃	7	18,4	23	60,5	7	18,4	1	2,6	0	0,0	
Female . . .	M ₁	0	0,0	7	10,3	46	67,6	15	22,1	0	0,0	
	M ₂	4	8,2	32	65,3	10	20,4	3	6,1	0	0,0	
	M ₃	8	21,6	24	64,9	2	5,4	3	8,1	0	0,0	
Combined . . .	M ₁	0	0,0	20	15,4	82	63,1	28	21,5	0	0,0	
	M ₂	6	6,0	71	71,0	18	18,0	5	5,0	0	0,0	
	M ₃	15	20,0	47	62,7	9	12,0	4	5,3	0	0,0	

No significant sexual difference in the expression of metaconid cristid morphology is shown by the San, and in the Negro no statistically significant sexual difference in metaconid cristid morphology is shown on the second and third molars. On the first permanent molar, however, the Negro female shows a significantly higher frequency of deflecting wrinkles than does the male ($X^2 = 4,82$; $p < 0,05$).

In both the Negro and the San the principal cristid of the metaconid of the first molar is most commonly well developed and straight. The main metaconid cristids of the second and third molars of both populations are most frequently weakly developed and are not deflected (Table 16).

The frequency of deflected metaconid cristids in both sexes of both populations is considerably higher on the first molar than on either the second or third molars. In the Negro (both sexes) and in the San female the metaconid crest of the second molar is deflected somewhat less frequently than on the third molar. In the San male the frequency of deflecting wrinkles on the M₂ is slightly higher than on the M₃. In the sexually pooled San sample the second and third molars show nearly identical frequencies of deflected metaconid cristids.

There is no significant difference between the San male and the Negro male in the frequencies of deflecting wrinkles on any of the lower molars, nor is there any significant difference between the San female and Negro female frequencies on the first and third molars. However, whereas no Negro female M₂ was found to possess a deflecting wrinkle, this feature was expressed on

some 6,1 per cent of San female second molars ($X^2 = 6,49$; $p < 0,025$). Comparisons of sexually pooled data indicates that no significant difference exists between the South African Negro and the Kalahari San in the frequency of expression of deflecting wrinkles on either the first or third molars. The San possesses a deflecting wrinkle on the second molar in a significantly higher percentage of cases on the second mandibular molar ($X^2 = 4,45$; $p < 0,05$).

Morris (1970) noted that the presence of a metaconid deflecting wrinkle may effect a metaconid-hypoconid contact. In the Negro male a deflecting wrinkle and a metaconid-hypoconid contact (Y pattern) were found together in only 16,2 per cent of first molars, 1,5 per cent of second molars, and 7,7 per cent of third molars. These two features were found together on the first, second and third molars of the Negro female in 24,4 per cent, 0,0 per cent, and 8,3 per cent of cases respectively. In the San male they were encountered together on 21,2 per cent of first, 7,4 per cent of second, and 0,0 per cent of third molars. The incidences of concomitant expression of these two characters in the San female molars are similar to the frequencies encountered on the San male teeth. Suzuki & Sakai (1965*b*), in a study of the deflecting wrinkle on the first lower molars of recent Japanese, recorded that this character was present in 49,3 per cent of male and 23,8 per cent of female teeth exhibiting a Y pattern.

It is clear that there is no interdependence of the deflecting wrinkle and the Y pattern on the lower molars of the South African Negro and the San. However, as pointed out above, Morris (1970), amongst others (e.g. Hanihara 1961; Hanihara *et al.* 1975; Turner & Hanihara 1977; Turner 1976, 1979; Turner & Swindler 1978), has erroneously identified a strongly developed, straight metaconid crest as a deflecting wrinkle. A highly significant ($p < 0,005$) relationship between occlusal pattern and metaconid crest morphology was found on all the lower molars of both sexes of the Negro and San, but the Y pattern (a metaconid-hypoconid contact) was found to be dependent upon the presence of a large, *straight* metaconid crest.

Reported frequencies of deflecting wrinkles on the lower molars of various human populations are tabulated in Table 17. It is apparent that the majority of authors have classified both straight, well-developed metaconid crests and truly deflected cristids as deflecting wrinkles.

Morris (1970) reported that 46,3 per cent of South African Negro and 78,5 per cent of San first molars show a deflecting wrinkle. By combining straight, well-developed crests and deflected metaconid cristids into a single category—'deflecting wrinkle'—as advocated by Morris (1970) and others, some 68,9 per cent of Negro and 84,6 per cent of San first molars examined by the present author were found to evince this feature (Table 17). The figures (combined) are somewhat, albeit insignificantly, higher than those reported by Morris (1970) for the same populations. Comparison of the results obtained by authors who have followed this method of classification (Table 17: frequencies preceded by x) reveals that only the Amerindian (Morris 1970),

Chinese (Turner 1976), and Wajin (Hanihara *et al.* 1975) show a 'deflecting wrinkle' on the first molar more commonly than does the South African Negro. Only the Chinese (Turner 1976) show a higher frequency of this character than the San on the M_1 .

TABLE 17

Incidence of metaconid deflecting wrinkle on lower permanent molars reported for various human populations. Sexes combined.

Group	Population		M_1	M_2	M_3	Reference
Mongoloid	Amerindian	*	74,8			Morris 1970
			29,6			Hanihara <i>et al.</i> 1964
	Japanese		23,4			Suzuki & Sakai 1956b
		*	31,6			Turner 1976
	Ainu	*	54,2	0,0	0,0	Turner 1976, 1979
		*	51,2			Turner 1976
		*	51,2	10,7	3,6	Turner & Hanihara 1977
		*	87,5			Turner 1976
	Chinese	*	71,6			Hanihara <i>et al.</i> 1975
	Wajin	*	71,6			Hanihara <i>et al.</i> 1975
Melanesian	New Britain	*	60,0	5,4	0,0	Turner & Swindler 1978
Caucasoid	European	*	34,2			Axelsson & Kirveskari 1977
	South African*		7,0			Morris 1970
	Indian	*	11,3			Morris 1970
Negroid	South African*		46,3			Morris 1970
		*	68,9	7,1	8,9	Present study
			19,0	1,5	4,4	Present study
Khoisanoid	San	*	78,5			Morris 1970
		*	84,6	23,0	17,3	Present study
			21,5	5,0	5,3	Present study

* Frequencies include straight, well-developed metaconid crest as well as true deflecting wrinkles.

If one considers only those studies in which a truly deflected metaconid crest has been classified as a deflecting wrinkle, the Negro and San frequencies of this character are considerably lower (19,0 and 21,5 per cent respectively), as are the incidences reported for Mongoloid peoples (Suzuki & Sakai 1956b; Hanihara *et al.* 1964) (Table 17 herein). The frequencies of true deflecting wrinkles on the first lower molars of the South African Negro and San are only slightly lower than those reported for Japanese populations.

It has been suggested (Hanihara 1963, 1966, 1967, 1968a, 1968b, 1970; Hanihara *et al.* 1964) that the deflecting wrinkle be included in the 'Mongoloid dental complex' of both the deciduous and permanent teeth. From the foregoing it is apparent that, regardless of whether a straight, strongly developed metaconid crest and a deflected crest or only a truly deflected metaconid crest is classified as a deflecting wrinkle, the frequencies of this feature on the San and Negro molars are within the range of frequencies recorded for Mongoloid peoples. Axelsson & Kirveskari (1977) have suggested that the inclusion of the deflecting wrinkle in the 'Mongoloid dental complex' be re-evaluated. It is evident that the racially diagnostic value of this feature in itself is doubtful,

but it forms only part of the 'Mongoloid dental complex' as defined by Hanihara. More particularly, this complex consists of concomitantly high expressions of (i) shovelled incisors, (ii) tuberculum intermedium on the dm_2 and M_1 , (iii) tuberculum sextum on the dm_2 , (iv) protostylid on the dm_2 , (v) plagiocnule (metaconule) on the dm_2 , and (vi) deflecting wrinkle on the dm_2 and M_1 . The high frequencies of one of these characters (e.g. a deflecting wrinkle) in non-Mongoloid populations does not necessarily detract from its significance as a part of a complex of other features.

The frequencies of the tuberculum sextum recorded for the permanent lower molars of the South African Negro and San are presented in Table 18. No significant sexual dimorphism in the possession of this accessory cuspid is present in either the San or Negro samples examined.

TABLE 18

Incidence of tuberculum sextum on lower permanent molars of the South African Negro and Kalahari San.

Population	Sex	M_1		M_2		M_3	
		N	%	N	%	N	%
Negro	Male	12	5,2	15	5,1	58	19,9
	Female	6	6,4	2	1,9	19	22,1
	Combined . . .	18	5,5	17	4,3	77	20,4
San	Male	10	16,4	6	14,3	6	20,7
	Female	10	15,4	5	12,2	14	38,9
	Combined . . .	20	15,9	11	13,2	20	30,8

While the Negro and San males show a tuberculum sextum on the third molars in a nearly identical percentage of cases, the San male possesses this cuspid significantly more frequently on the first molar ($X^2 = 8,83$; $p < 0,005$) and the second molar ($X^2 = 5,29$; $p < 0,025$). The San female tends to possess a tuberculum sextum more frequently than the Negro female on all three mandibular molars and, while the occurrences are not significantly different on the first and third molars, the San female has this cuspid in a significantly higher frequency on the second molar ($X^2 = 6,75$; $p < 0,01$). Comparison of the sexually pooled data reveals that the San shows a significantly higher incidence of the tuberculum sextum on the first molar ($X^2 = 12,72$; $p < 0,005$) and second molar ($X^2 = 10,11$; $p < 0,005$). The San also tends to show this cuspid more frequently than the Negro on the third molar, but the difference in this instance was found to be statistically not significant.

Jacobson (1967) recorded the frequency of a tuberculum sextum on the permanent lower molars of the South African Negro, but he did not mention the criteria by which he classified this cuspid. His figures for the occurrence of the tuberculum sextum in this population are consistently (albeit insignificantly) lower than those in this study for all the molars. The differences amongst these figures may reflect different sample sizes, different methods of classifi-

cation, or the fact that Jacobson (1967) scored teeth from both sides of the same jaw in a number of instances. Kiernberger (1955) recorded the presence of this cuspid in her Khoisanoid sample, but she did not differentiate between it and the tuberculum intermedium. She combined the occurrence of either one or both into a single molar classification.

Frequencies of the tuberculum sextum recorded by other workers for the lower molars of various human populations are presented in Table 19. This

TABLE 19

Percentage frequencies of tuberculum sextum on permanent lower molars reported for various human populations. Sexes combined.

Group	Population	M_1	M_2	M_3	Reference
Mongoloid	Amerindian . .	49,0	14,5		Brewer-Carias <i>et al.</i> 1976
		6,0	16,0	32,0	Hellman 1928
		3,3	2,6	4,8	Nelson 1938
	Eskimoid . . .	1,0	20,0	28,0	Hellman 1928
		1,2	10,3	16,0	Pedersen 1949
	Chinese . . .	0,0	0,0	0,0	Hellman 1928
		31,0			Turner 1976
	Japanese . . .	21,7			Hanihara 1970
		18,4			Suzuki & Sakai 1957
		5,6	1,6		Takehisa 1957
		25,3			Turner 1976
		58,0			Turner 1976
	Ainu	58,0	14,0	27,5	Turner 1979
		17,8			Hanihara 1970
		21,7			Suzuki & Sakai 1957
		29,8			Turner 1976
		25,8	8,5	9,1	Turner & Hanihara 1977
	Polynesian . . .	54,5	30,0	50,0	Suzuki & Sakai 1973
	Hawaiian . . .	43,0	2,0	4,0	Katich & Turner 1975
	Easter Island . .	19,0	9,0	14,0	Turner & Scott 1976
	Yapese	71,0	77,0	80,0	Harris <i>et al.</i> 1975
Australoid	Austral. Aborigine	8,0	43,0	54,0	Hellman 1928
Melanesian	Melanesian . .	9,0	5,0	9,0	Dahlberg 1961
	New Britain . .	32,5	9,8	24,2	Turner & Swindler 1978
Caucasoid	European . . .	17,0	10,9		Axelsson & Kirveskari 1979
	American . . .	0,0	0,0	3,0	Hellman 1928
		0,0	0,0		Takehisa 1957
Negroid	East African . .	6,6	0,3	2,0	Chagula 1960
	West African . .	3,0	6,0	16,0	Hellman 1928
	South African . .	5,5	4,3	20,4	Present study
	American . . .	2,0	8,0	33,0	Hellman 1928
Khoisanoid	San	15,9	13,2	30,8	Present study

table does not include all the references for recent human samples as some workers have combined the presence of a tuberculum sextum and a tuberculum intermedium into a single category (e.g. Goldstein 1931; Berry 1976). Others have recorded the presence of cusp numbers over five but have not stated whether the tuberculum sextum was, indeed, always the sixth cusp (e.g. Goldstein 1948; Thomsen 1955; Matsuda 1961; Brabant & Tweisselmann 1964;

Devoto & Cigliano 1970; Brabant 1971; Devoto & Perrotto 1972; Perzigian 1976).

Examination of Table 19 indicates that the first lower molars of the South African Negro possess a tuberculum sextum about as often as the M_1 's of the east African Negro and slightly more frequently than the molars of the west African Negroes. The frequency of the presence of the tuberculum sextum on Negro first molars tends to be relatively low. The San first molars exhibit this cuspid more frequently than do the Negro teeth. Whereas Hellman (1928) and Takehisa (1957) recorded a complete absence of this cuspid in their American Caucasoid first molar samples, Axelsson & Kirveskari (1979) reported that 17.0 per cent of Icelandic Caucasoids examined by them possessed a tuberculum sextum on the first molar. Sometimes dramatic differences in the frequency of the tuberculum sextum on the first lower molars of various Mongoloid peoples have been recorded (Table 19). However, the incidences of this cuspid in a number of Mongoloid populations are considerably higher than those recorded for Negroid, Khoisanoid, Caucasoid, Australoid, and Melanesian peoples.

Generally, it appears that the first molars of Negroid, Khoisanoid, Caucasoid, and Australoid peoples show a relatively low incidence of accessory distal cuspulids, the Melanesians tend to have a somewhat higher incidence of this feature, while the tuberculum sextum appears to be present most commonly on the first molars of Mongoloid populations. The same interpopulational differences tend to exist with regard to the incidence of this cuspid on the second permanent molars, the most notable exception being the Australoid peoples, who have this feature relatively frequently on this tooth. With regard to the third mandibular molar, the Caucasoid populations tend to exhibit a tuberculum sextum less frequently than most others and, again, the incidence of this cuspid on the M_3 is greater in Mongoloid populations than in others.

It would appear that there is no consistent relationship between the frequency of accessory distal cuspulids on the first, second and third molars within populations. That is, a tuberculum sextum appears to occur in declining order of frequency on M_1 - M_2 - M_3 respectively about as often as on M_3 - M_2 - M_1 respectively (Table 19). However, in all population studies in which all three molar types were examined, the third molar was found to possess a tuberculum sextum more commonly than the second molar. Although the third molar shows a higher frequency of five cusps than does the second molar, this can hardly be related to the higher incidences of tubercula sextum in the third molar, as the first molar, which shows the highest frequency of five cusps, has a tuberculum sextum in a higher percentage of cases than the M_2 in about the same number of populations in which the second molar shows this cuspid more frequently than the M_1 (Table 19).

The South African Negro and San both show the tuberculum sextum most frequently on the third molar, followed in descending order by the first and second molars respectively. Of the other three Negro populations examined

(Table 19), two (west African and American) have molar frequency orders of the tuberculum sextum of M_3 - M_2 - M_1 , while the third (east African) has a molar frequency order of M_1 - M_3 - M_2 .

The frequencies of the tuberculum intermedium recorded for the South African Negro and Kalahari San are given in Table 20. The Negro female shows this accessory lingual cuspid more frequently than the Negro male on all three molars. The San female tends to have a tuberculum intermedium more often than the San male on the first molar but less frequently than the male on the third molar. However, the sexual differences in both populations are slight and not statistically significant.

TABLE 20

Incidence of tuberculum intermedium on lower permanent molars of the South African Negro and Kalahari San.

Population	Sex	M_1		M_2		M_3	
		N	%	N	%	N	%
Negro	Male	32	13,1	4	1,3	30	10,0
	Female	18	17,8	2	1,9	12	13,6
	Combined . . .	50	14,5	6	1,5	42	10,8
San	Male	11	17,7	0	0,0	3	7,9
	Female	16	22,5	0	0,0	2	4,9
	Combined . . .	27	20,3	0	0,0	5	6,3

The South African Negro shows a tuberculum intermedium less frequently on the first molar but more frequently on the third molar than does the San. Only 1,5 per cent of Negro second molars were found to show this cuspid, while no San M_2 evinced a tuberculum intermedium. The frequency differences on all molars amongst these two populations are slight and not statistically significant.

Jacobson (1967) recorded the presence of the tuberculum intermedium for the South African Negro and, although he gave no indication of the criteria used in the recording of this feature, his data are similar to those reported here. Jacobson's frequencies are, however, consistently (albeit slightly) larger than those given here. These discrepancies are probably due to the fact that different classificatory standards may have been employed, and also that Jacobson (1967) counted teeth rather than individuals.

In her study of Khoisan teeth, Kiernberger (1955) recorded the frequencies of accessory cusps on the lower molars, but did not differentiate between the tuberculum sextum and tuberculum intermedium. Rather, she regarded the presence of either one or both on a molar as constituting a single crown category.

Numerous workers have, like Kiernberger (1955), recorded the presence of additional cuspulids and have not separated the tuberculum intermedium and the tuberculum sextum (Hrdlička 1910; Janzer 1927; Rosenzweig & Zilberman 1967, 1969; Sofaer, MacLean & Bailit 1972; Sofaer *et al.* 1972; Berry 1976).

Frequencies of the tuberculum intermedium recorded for the permanent lower molars of various human populations are tabulated in Table 21. A

TABLE 21

Percentage frequencies of tuberculum intermedium on permanent lower molars reported for various human populations. Sexes combined.

Group	Population	M_1	M_2	M_3	Reference
Mongoloid	Amerindian . . .	6,6	0,0	2,0	Nelson 1938
		0,0	0,0	6,0	Hellman 1928
	Eskimoid . . .	0,0	0,0	0,0	Hellman 1928
		0,0	0,7	0,0	Pedersen 1949
	Chinese . . .	0,0	5,0	0,0	Hellman 1928
			12,0	8,0	De Terra 1905
	Japanese . . .	11,8			Turner 1976
		6,7			Hanihara 1970
		0,3			Suzuki & Sakai 1957
		5,7	0,2		Suzuki & Sakai 1956c
		6,7			Turner 1976
		1,5			Turner 1976
	Ainu	58,0	14,0	27,5	Turner 1979
		4,3			Hanihara 1970
		0,0			Suzuki & Sakai 1957
		4,3			Turner 1976
	Polynesian . . .	4,3	0,0	2,9	Turner & Hanihara 1977
		23,0	14,0	17,0	Turner & Scott 1976
	Hawaiian . . .	7,0	1,1		Suzuki & Sakai 1973
		15,0	7,0	3,0	Katich & Turner 1975
	Yapese	31,0	12,0	20,0	Harris <i>et al.</i> 1975
Australoid	Austral. Aborigine	0,0	0,0	0,0	Hellman 1928
		6,3			De Terra 1905
Melanesian	Melanesian . . .	9,0	5,0	9,0	Dahlberg 1961
	Papuan			20,0	De Terra 1905
	New Britain . . .	10,9	0,0	8,8	Turner & Swindler 1978
Caucasoid	European . . .	1,5	1,0	2,6	De Terra 1905
		15,5	2,5		Axelsson & Kirveskari 1979
	American	3,0	2,0	0,0	Hellman 1928
Negroid	West African . . .	2,0	5,0	6,0	Hellman 1928
	South African . .	14,5	1,5	10,8	Present study
	American	22,0	4,0	13,0	Hellman 1928
Khoisanoid	San	20,3	0,0	6,3	Present study

Note that the percentage frequencies recorded for the San and South African Negro are not strictly comparable with the results of a number of these studies because different definitions of cuspal presence were used.

number of workers whose data are presented in Table 21 regarded a post-metaconulid, an entoconulid and/or a large, separate median lingual cuspid as a tuberculum intermedium. Had the present author also subscribed to the recognition of all three these features, instead of only the third, as a tuberculum intermedium it is certain that the percentage frequencies would have been higher than those presented in Table 20. Even so, the incidences of the cuspid on the first molars of the San and South African Negro are comparatively high. Of the twenty-nine populations in which first molars have been examined for this feature (Table 21), six have higher frequencies than the South African Negro (Japanese of Turner 1979; Polynesians of Turner & Scott 1976; Hawaiians of Katich & Turner 1975; Yapese of Harris *et al.* 1975; Icelandic Caucasoids of Axelsson & Kirveskari 1979; American Negroes of Hellman

1928). Of these populations, only four have a greater percentage incidence than the San (Japanese of Turner 1979; Polynesians of Turner & Scott 1976; Yapese of Harris *et al.* 1975; American Negroes of Hellman 1928). It should be noted that there are rather dramatic differences amongst the frequencies of M_1 cusplids reported for Jomon Japanese by Turner (1979) and other Japanese populations, between the frequencies reported for Polynesians by Turner & Scott (1976) and Suzuki & Sakai (1973), and between the Icelandic Caucasoids (Axelsson & Kirveskari 1979) and other European and American Caucasoid populations. It is possible that the frequencies recorded by Turner (1979), Turner & Scott (1976), Harris *et al.* (1975), and Axelsson & Kirveskari (1979) are inflated because of the classificatory criteria employed by them.

The incidences and frequencies of the presence of a fovea anterior on the lower molars of the San and South African Negro are presented in Table 22.

TABLE 22
Incidence of fovea anterior on lower permanent molars of the
South African Negro and Kalahari San.

Population	Sex	M_1		M_2		M_3	
		N	%	N	%	N	%
Negro	Male	148	69,8	167	57,8	144	50,0
	Female	62	69,7	69	67,6	54	63,5
	Combined	210	69,8	236	60,4	198	53,1
San	Male	52	91,2	41	82,0	12	35,3
	Female	43	76,8	27	61,4	12	35,3
	Combined	95	84,1	68	72,3	24	35,3

The first molars of the Negro male and female show this feature in an almost identical percentage of cases and, while the female possesses a fovea anterior on the second molar more commonly than does the male, this difference is statistically insignificant. The frequency of this fossid on the third molar is significantly greater in the Negro female ($X^2 = 4,82$; $p < 0,05$) than in the male. On the other hand, the fovea anterior is present on the first and second molars significantly more frequently ($X^2 = 4,40$; $p < 0,05$ and $X^2 = 4,98$; $p < 0,05$ respectively) in the San male than in the San female. While a significant degree of sexual dimorphism in the presence of this fossid is apparent in the third molars of the Negro, both sexes of the San show the same frequency of the fovea anterior on the wisdom teeth. In all instances where significant sexual dimorphism was apparent, the differences were barely significant.

The fovea anterior and cusp number were found to be independent variables on all three molars of the San, on the first molars of the Negro and on the third molars of the Negro female. These two features were found to be dependent on the second molars of the Negro male ($X^2 = 4,19$; $p = 0,04$) and the Negro female ($X^2 = 7,92$; $p = 0,005$) and on the third molars of the Negro male ($X^2 = 12,22$; $p = 0,002$). In these latter three instances the fovea anterior tends to be present on five cusped teeth and absent on molars with only four cusps.

The San male possesses a fovea anterior significantly more frequently than the Negro male on both the first ($X^2 = 10,80$; $p < 0,005$) and second ($X^2 = 10,54$; $p < 0,005$) molars. The San male shows this fossid less frequently than the Negro male on the third molar, but this difference is not statistically significant.

The Negro female possesses a fovea anterior less commonly than the San female on the first molar but more frequently on the second molar; these differences are slight, however, and are statistically insignificant. The Negro female displays this fossid more frequently than the San female on the third molar ($X^2 = 7,84$; $p < 0,01$).

Notwithstanding the sexual dimorphism apparent in the expression of the trigonid basin in both the San and Negro, the data were pooled for purposes of overall comparison (Table 22). The San displays a fovea anterior significantly more frequently than does the Negro on both the first ($X^2 = 8,67$; $p < 0,005$) and second ($X^2 = 4,65$; $p < 0,05$) mandibular molars. Conversely, the Negro possesses this mesial fossid significantly more frequently than the San on the third molar ($X^2 = 7,28$; $p < 0,01$).

In both populations, and in both sexes of these populations the first molar shows the highest frequency of mesial fossids, following in decreasing order of commonality by the second and third molars respectively.

The incidences and frequencies of the fovea posterior on the mandibular molars of the South African Negro and Kalahari San are presented in Table 23. No significant sexual dimorphism in the presentation of this character on any of the molars was found within either the San or Negro samples.

TABLE 23
Incidence of fovea posterior on lower permanent molars of the
South African Negro and Kalahari San.

Population	Sex	M_1		M_2		M_3	
		N	%	N	%	N	%
Negro	Male	29	12,7	37	12,7	47	16,3
	Female	19	21,3	15	14,3	15	17,4
	Combined . .	48	15,1	52	13,1	62	16,6
San	Male	11	20,4	3	7,1	0	0,0
	Female	10	19,2	4	10,0	1	2,8
	Combined . .	21	19,8	7	8,5	1	1,5

The San male shows the distal fossid more frequently than the Negro male on the first molar, while the Negro male possesses a fovea posterior more commonly on the second molar; these differences are slight and not statistically significant. The Negro male displays a fovea posterior significantly more frequently than does the San male on the third molar ($X^2 = 5,56$; $p < 0,025$).

The San female displays this distal fossid less frequently than does the Negro female on all three molars; the differences with regard to the first and second molars are slight and statistically insignificant. The Negro female frequency is significantly higher on the third molar ($X^2 = 4,79$; $p < 0,05$).

Comparison of the sexually pooled data (Table 23) indicates that, while the San tends to show a fovea posterior more commonly than the Negro on the first molar, the Negro has a higher frequency of this fossid on the second. These differences are slight and not statistically significant. The Negro possesses a significantly higher frequency of the fovea posterior than does the San on the third molar ($X^2 = 10.19$; $p < 0.005$).

Chi-square evaluation of the fovea posterior and cusp number revealed these two features to be independent on all three molars of both sexes of the San and Negro.

It is apparent that the fovea anterior is considerably more common than the fovea posterior on all lower molars of the San and Negro (cf. Tables 22-23).

Biggerstaff (1968) recommended that the combination of the presence or absence of the fovea posterior and cuspal number was a more useful criterion for the classification of lower molars than the traditional occlusal patterns. In a study of dental casts of 199 pairs of like-sexed twins he (Biggerstaff 1975) found that males had a significantly higher frequency of molars with five cusps and fovea posterior (his '5fd' type) than did females. In the present samples of Negro and San molars, however, females possess a higher frequency of '5fd' molars, except for the Negro M_3 and the San M_2 , in which instances the female frequencies are slightly lower than those exhibited by the male. It has been shown that cusp number and the fovea posterior are independent variables (at least on the Negro and San molars). In addition, both sexes of the San and Negro exhibited four-cusped molars with the fovea posterior. Thus, Biggerstaff's (1968, 1975) method of crown classification appears to be incomplete, and even if complete it would serve no more useful purpose than the classification of molars according to the 'traditional' cusp-groove pattern relationships.

It has been claimed that 'the tuberculum sextum probably appears most frequently on five-cusped teeth having a distal fovea and distal marginal ridge' (Biggerstaff 1968: 444). Quite the contrary is evident in the Negro and San lower molars. In the majority of cases the tuberculum sextum and the fovea posterior do not occur together on the same tooth, probably because a tuberculum sextum (especially a large cuspid) obliterates the distal fossid by filling up the distolingual corner of the crown (Robinson 1956).

The presence of crenulate or wrinkled enamel was recorded here for the lower molars of the South African Negro and San (Table 24).

In the Negro, the female shows a higher frequency of crenulate enamel than does the male on all three molars. The degree of sexual dimorphism in enamel appearance on the first and second molars is slight and the differences are not statistically significant. In the third molar, however, the frequency of crenulate enamel in females is significantly greater than that in males ($X^2 = 10.18$; $p < 0.005$).

The San male shows crenulate enamel more commonly than the San female on the first molar, but on the second and third molars the female tends to

TABLE 24
Incidence of crenulate enamel on lower permanent molars of the
South African Negro and Kalahari San.

Population	Sex	M_1		M_2		M_3	
		N	%	N	%	N	%
Negro	Male	11	4,5	13	4,3	60	19,9
	Female	7	6,9	8	7,5	32	36,4
	Combined . .	18	5,2	21	5,1	92	23,6
San	Male	2	3,3	1	2,1	3	8,6
	Female	1	1,8	1	2,7	3	9,4
	Combined . .	3	2,6	2	2,4	6	9,0

possess crenulate enamel more frequently. The sexual differences amongst the lower molars of the San are slight and statistically insignificant.

The Negro male tends to possess wrinkled enamel more frequently than the San male on all three mandibular molars, but in no instance was the difference in frequency between them found to be statistically significant. The Negro female shows crenulate enamel more commonly than the San female on all molars, and while the differences in frequency on the first and second molars are insignificant, in the third lower molar the Negro female incidence is significantly greater than that of the San female ($X^2 = 8,27$; $p < 0,005$). Thus, the Negro tends to possess crenulate enamel more commonly than does the San on all three permanent mandibular molars. The Negro frequencies are only slightly higher than those of the San for the first and second molars, and in these instances the sexually pooled population differences are not statistically significant. The third molar of the Negro is crenulate in appearance considerably more often than is this tooth in the San, and here the differences in frequencies are statistically significant ($X^2 = 7,23$; $p < 0,01$).

Crenulate enamel on the lower molars of both the San and Negro appears to be more common on the third molar than on either of the mesial two molars. In both populations the expression of crenulate enamel by the first and second molars is nearly of the same frequency.

Due to the inherent difficulty of objectively classifying crenulate enamel, the number of observations of this feature recorded for recent human teeth is understandably low. Jacob (1967) stated that he believed enamel wrinkling to be a characteristic feature of Mongoloid dentitions. Kiernberger (1955: 31) maintained that 'das wichtigste Charakteristikum des Khoisanidenzahnes ist die von Adloff festgestellte Schmelzrunzelung der Molarenkrone'. The frequencies recorded here for the San molars certainly do not support Kiernberger's statement; rather, they imply quite the contrary.

Pedersen (1949: 103) recorded that 'pronounced wrinkles on the occlusal surfaces were seen in seven out of twenty lower third molars in the skulls [a frequency of 35,0 per cent—cf. Negro female incidence] and in many cases of the living Eskimo'. He noted also that these wrinkles were absent on all first and second molars examined by him, but that the wear shown by these teeth had probably eradicated any trace of enamel wrinkles.

It is evident that smooth occlusal enamel is characteristic of the lower molars of the San, and of the first and second molars of the South African Negro. The third molar of the Negro (especially of the female) tends to show a higher incidence of secondary and tertiary enamel cristids, but even here the incidence cannot be considered to be high.

DISCUSSION

SEXUAL DIMORPHISM

Significant sexual dimorphism in the morphology of the permanent mandibular molars is relatively low in both the San and the South African Negro. Such dimorphism is expressed in only three of the eight features examined: the deflecting wrinkle, the fovea anterior, and the presence of crenulate enamel (Table 25). The incidences of metaconid deflecting wrinkles were significantly dimorphic on only the first molar of the Negro, while the incidences of crenulate enamel were found to be significantly different on only the third molar of the Negro. Significant sexual dimorphism is expressed most commonly with regard to the fovea anterior. The sexual incidences of this feature are significantly different on the first and second molars of the San and on the third molars of the Negro. Of the five instances of significant sexual dimorphism found in the Negro and San molars (Table 25) the sexual differences were barely significant in four. A highly significant degree of sexual dimorphism is shown only by the incidence of crenulate enamel on the Negro third molars. However, crenulate enamel is very difficult to classify objectively; enamel wrinkles may be obliterated by slight wear, and the genetic factors influencing the expression of these wrinkles may be easily overshadowed by environmental factors such as dietary fluorine intake, disease, and nutritional status.

TABLE 25

Summary of morphological features in which significant sexual dimorphism was demonstrated in the South African Negro and Kalahari San.

Character	M_1		M_2		M_3	
	Negro	San	Negro	San	Negro	San
1	—	—	—	—	—	—
2	—	—	—	—	—	—
3	—	—	—	—	—	—
4	—	—	—	—	—	—
5	b	—	—	—	—	—
6	—	b	—	b	b	—
7	—	—	—	—	—	—
8	—	—	—	—	a	—

a—significant difference at $p < 0.005$;

b—significant difference at $p < 0.05$.

Characters: 1—principal cusp number; 2—tuberculum sextum; 3—tuberculum intermedium; 4—primary occlusal pattern; 5—deflecting wrinkle; 6—fovea anterior; 7—fovea posterior; 8—crenulate enamel.

Thus, there is a rather low incidence and degree of sexual dimorphism in the features examined here on the lower permanent molars of the South African Negro and Kalahari San. The dimorphism shown by these populations is comparable to, or perhaps slightly less than, that described for the permanent mandibular molars of other population groups. De Villiers (1958) examined the expression of sexual dimorphism in some sixty-seven non-metrical features of the South African Negro skull. She found that significant sexual differences are manifest in only fourteen of these features, and that sexual dimorphism is largely associated with the face and jaws and it is most pronounced in mandibular characters. De Villiers (1968) concluded that the amount of sexual dimorphism displayed in the skull of the South African Negro is comparable to, or slightly less than, that shown by other groups.

CHARACTERISTICS OF SAN AND NEGRO MOLARS

While both the incidence and degree of sexual dimorphism within the San and Negro molars appear to be rather low, the significant differences in the morphological characters of the three mandibular molars amongst these two populations are more common (Table 26). Thus, seven of eight morphological features examined show significant interpopulational differences variously on one or more of the permanent molars. Two features (fovea posterior and crenulate enamel) have significant interpopulational differences on the third molar only, one feature (fovea anterior) shows significant San-Negro differences on all three molars, one character (tuberculum sextum) is significantly different on the first and second molars, and some three non-metrical features (principal cusp number, primary occlusal pattern, and deflecting wrinkle) show significant interpopulational differences on only the second molar. Of the ten instances of significant interpopulational differences encountered, only two (deflecting wrinkle and fovea anterior on the M_2) were found to be barely significant statistically (Table 26).

In the first molar only two of eight features show significant differences of incidence between the San and Negro, three features on the third molar display such differences while five characters show significant populational differences on the second molar. Thus, the fovea anterior and the tuberculum sextum appear to be respectively the first and second most useful discriminatory characters of the mandibular molars, while the second molar seems to display the greatest number of differences between the San and South African Negro populations (Table 26).

On the basis of the foregoing analyses a general characterization of the morphology of the permanent mandibular molars of the San and South African Negro may be summarized. In view of the relatively low degree of sexual dimorphism apparent in the features examined, the characterizations presented here refer to sexually pooled population samples and sexual differences are enumerated only in those instances where they proved to be statistically signifi-

TABLE 26

Summary of morphological features in which significant (sexually pooled) population differences amongst the South African Negro and Kalahari San were demonstrated.

Character	M_1	M_2	M_3
1	—	a	—
2	a	a	—
3	—	—	—
4	—	a	—
5	—	c	—
6	a	c	b
7	—	—	a
8	—	—	b

a—significant difference at $p < 0,005$;

b—significant difference at $p < 0,01$;

c—significant difference at $p < 0,05$.

Characters: 1—principal cusp number;

2—tuberculum sextum; 3—tuberculum inter-

medium; 4—primary occlusal pattern;

5—deflecting wrinkle; 6—fovea anterior;

7—fovea posterior; 8—crenulate enamel.

cant. Lest these characterizations of lower molar morphology be viewed as typological, the frequencies of each trait are alluded to by the use of terms such as 'almost always', 'usually' and 'generally'. Arbitrarily defined frequency limits have been assigned to these terms as they are used here; thus, 'almost always' indicates a frequency between 90–100 per cent, 'usually' indicates a frequency between 80–90 per cent, and 'generally' refers to an incidence of between 70–80 per cent.

FIRST PERMANENT MOLAR

Negro: almost always five-cusped; tuberculum sextum usually to almost always absent; tuberculum intermedium usually absent; primary occlusal pattern generally to usually in the form of a Y; metaconid cristid generally either straight and strongly or straight and weakly developed in male and commonly strongly developed in female with deflecting wrinkle usually absent in the male and generally absent in the female; fovea anterior generally present; fovea posterior usually absent; occlusal surface enamel usually to almost always smooth.

San: almost always five-cusped; tuberculum sextum usually absent but present significantly more often than in the Negro; tuberculum intermedium generally or usually absent; primary occlusal pattern usually in the form of a Y; metaconid cristid generally either straight and strongly or straight and weakly developed with deflecting wrinkle generally to usually absent; fovea anterior almost always present in the male and generally present in the female and present significantly more often than in the Negro; fovea posterior generally to usually absent; occlusal surface enamel almost always smooth.

SECOND PERMANENT MOLAR

Negro: almost equally five or four-cusped; tuberculum sextum almost always absent; tuberculum intermedium almost always absent; primary occlusal pattern more commonly in the form of a +; metaconid cristid usually either weakly developed or absent with a deflecting wrinkle almost always absent; fovea anterior somewhat more commonly present than absent; fovea posterior usually absent; occlusal enamel usually to almost always smooth.

San: generally five-cusped, and significantly more frequently than in the Negro; tuberculum sextum usually absent but present significantly more frequently than in the Negro; tuberculum intermedium almost always absent; primary occlusal pattern almost equally in the form of either a Y or +, but significantly more frequently in the form of a Y than in the Negro; metaconid cristid generally straight and weakly developed and deflecting wrinkle usually to almost always absent, and with a significantly higher frequency of weak crests and a significantly lower incidence of deflecting wrinkles than in the Negro; fovea anterior usually present in the male and only somewhat more commonly present than absent in the female, present significantly more frequently than in the Negro; fovea posterior usually absent; occlusal enamel almost always smooth.

THIRD PERMANENT MOLAR

Negro: generally to usually five-cusped; tuberculum sextum generally to usually absent; tuberculum intermedium usually absent; primary occlusal pattern usually in the form of either a + or an X, with almost equal frequencies of both; metaconid cristid almost always either weakly developed or absent, with almost equal frequencies of both expressions; fovea anterior either present or absent with almost equal frequency in the male and somewhat more commonly present in the female; fovea posterior usually absent; occlusal enamel generally smooth.

San: generally to usually five-cusped; tuberculum sextum more commonly to generally absent; tuberculum intermedium usually absent; primary occlusal pattern generally either in the form of a + or an X with almost equal frequencies of both and, as in the Negro, with only a slightly lower incidence of the Y pattern; metaconid cristid usually either weakly developed or absent and, as in the Negro, a deflecting wrinkle is usually to almost always absent; fovea anterior more commonly absent than present and present significantly less frequently than in the Negro; occlusal enamel usually smooth, and crenulate in appearance significantly less frequently than in the Negro.

OCCLUSAL MORPHOLOGICAL INTERRELATIONSHIPS

Almost all of the features examined here show the same intermolar incidence relationships (e.g. a given character is most commonly expressed on the M_1 , less frequently shown by the M_2 and least commonly evinced by the M_3) in both the San and Negro. In both populations the five principal cusps, the

metaconid deflecting wrinkle and the tuberculum intermedium are most commonly shown by the first molar, followed in decreasing order of frequency by the third and second molars respectively (i.e. frequencies $M_1 > M_3 > M_2$). The fovea anterior and the Y pattern are expressed most frequently by the first molar, followed in decreasing incidences by the second and third molars respectively (i.e. $M_1 > M_2 > M_3$). Conversely, the tuberculum sextum and the X pattern are shown most commonly by the third molar, followed in decreasing order of frequency by the second and first molars respectively (i.e. $M_3 > M_2 > M_1$). In both the San and the Negro the H pattern is evinced only on third molars. Crenulate enamel is displayed most frequently on this tooth with considerably lower, and almost equal, frequencies shown by the first and second molars. The + pattern is shown most frequently by the second molars, while the third and first molars show decreasing frequencies of this pattern (i.e. $M_2 > M_3 > M_1$). With respect to the fovea posterior, however, this character shows a frequency relationship in the South African Negro of $M_3 > M_1 > M_2$ and in the San of $M_1 > M_2 > M_3$.

On all three molars of both the Negro and the San the fovea anterior is present more often than the fovea posterior. Also, in both populations, while the tuberculum intermedium is shown more frequently than the tuberculum sextum on the first molar, on the second and third molars the tuberculum sextum is present considerably more frequently than the tuberculum intermedium.

Paired chi-square evaluations of interdependence have been performed for most of the characters examined. In these evaluations either no interdependence or sometimes barely significant levels of dependence were found. Thus, in both the San and the South African Negro the principal cusp number and primary groove pattern appear to have a sometimes low level of dependence, but generally these two characters seem to be independent. The primary occlusal pattern appears to be independent of metaconid cristid morphology, and in particular, the Y pattern and the deflecting wrinkle are not dependent. The presence of neither the fovea posterior nor the fovea anterior is dependent upon principal cusp number. Similarly, the presence of crenulate occlusal enamel is independent of principal cuspal number on the lower molars of the San and South African Negro. Thus, until the type of genetic control over the expression of lower molar dental variants has been established, it would seem that each of these features should be categorized separately. That is, classificatory schemes that combine two or more characters (e.g. Y-5, +-4, X-5, 5fd, etc.) should not be used in odontological studies.

BIOLOGICAL INTERRELATIONSHIPS OF THE SOUTH AFRICAN NEGRO AND THE KALAHARI SAN

The term 'Khoisan' (or, as it is usually spelt, Khoisan) was proposed by Schultze-Jena (1928: 211) 'als gemeinsamer Rassenname für Hottentotten und Buschmänner'. The name Khoisan is most commonly used today in a generic

sense to include the Khoi (Hottentots) and the San (Bushmen). The biological interrelationship of the Khoisan (and especially the San) and African Negroes have been the subject of considerable study. Until about the middle of the present century, most workers were concerned with producing a classification or taxonomy of African peoples, and these workers generally expounded a typological approach to the problems of interrelationship definition. No useful purpose would be served here by reviewing these past polemics. More recently, studies of the Khoisan and Negro peoples have been based upon an examination of the limits of phenotypic variability of gross morphological features in these populations. Amongst the constellation of features thus examined a few of the more notable that serve to characterize the San are: mesometriocranial and pentaganoid cranium; mesoprosopic face and euryene upper face; orthognathism; mesochonch orbits; brachystaphaline palate; small postglenoid tubercles; faint glabella and weak supraciliary ridges; nasal bones highly obtusely angulated (De Villiers 1968); frontal processes of the maxillae highly obtusely angulated (Grine 1979); skin showing a lower mean reflectance and therefore lighter in colour than that of the Negro (Weiner *et al.* 1964); head hair tending to consist of tightly spiralled tufts; small, commonly lobeless ears with overrolled helices; relatively small stature (Tobias 1955-6, 1960, 1966; Singer & Weiner 1963); steatomeria and steatopygia (De Villiers 1961; Krut & Singer 1963); marked and nearly universal macronymphia (De Villiers 1961); ithyphally (Drury & Drennan 1926); fewer dermatoglyphic whorls and more arches; and high frequency of palmer patterns in areas II-IV (Tobias 1961). Tobias (1972), Nurse & Jenkins (1977), and Singer (1978) have compiled somewhat more extensive lists of gross morphological features that tend to characterize the San and delineate them from other African groups. Most, if not all, of the foregoing characters are probably polygenic and have complex modes of inheritance. In addition, the relationship between genotype and phenotype in not a few of these characters is made more complex by the modifying influences of the environment. Consequently, the assessment of these characters as genetic markers is extremely difficult.

Since the sixties the Khoisan and Negro peoples of southern Africa have been the subject of a number of genetic studies (Tobias 1966, 1972; Nurse & Jenkins 1977). The essential genetic unity of sub-Saharan Africa has been shown by these studies. More particularly, the strong genetic affinities of the South African Negro with the Negro populations of west and central Africa have been stressed (Tobias 1972). Although these genetic studies have demonstrated that the Khoisan peoples have more in common genetically with Negroes than either group has with non-African peoples, a number of differences between the San and Negro have been detected.

The $A^{\text{bantú}}$ phenotype was first characterized by Brain (1966) and thus named because he believed it to be characteristic of the South African Bantu-speaking Negro. Jenkins (1974) has shown this allele to be much commoner in the San (and Khoi) than in the southern African Negro and, because of its

virtual absence in Negroes to the north, he has postulated that the A^{bantu} red cell antigen is primarily a Khoisan character that has been acquired secondarily by Negro peoples in their southward migrations. Similarly, the Duffy red cell antigen, Fy^a , occurs with high frequency in the Khoisan, while Negroes often lack any Duffy antigen (Nurse & Jenkins 1977). Nurse & Jenkins (1977) have proposed that the Fy^a gene has been acquired by the southern African Negro from the Khoisan. Jenkins & Corfield (1972) have claimed that the acid phosphatase allele, Pr , is almost certainly a Khoisan marker, and it has been proposed that this gene was similarly acquired by the Negroes in the course of their southward migrations (Nurse & Jenkins 1977). However, Santachiara-Benerecetti *et al.* (1977) and Ojkutu *et al.* (1977) reported Pr frequencies of 0.17 and 0.05 in the Babinga Pygmies and the Yorba of Nigeria respectively, and, as such, this allele may not be a very useful marker in this context. Transferrin D_1 , a β -globulin variant, seems to represent an essentially San character in southern Africa, and its presence in southern African Negroes has been ascribed to San admixture (Nurse & Jenkins 1977).

In a survey of the distribution of variants of the 6-phosphogluconate dehydrogenase (6PGD) red cell enzyme in southern Africa, Jenkins & Nurse (1974) found that the PGD^c allele is not often present in San populations. They proposed that its presence in the San is an indication of Negro admixture. Glucose-6-phosphate dehydrogenase (G6PD) deficiency has been shown to be much less common in the San than in Negro populations (Charlton & Bothwell 1961). However, both of the characteristically Negro variants have been identified in the San, and this has been ascribed to Negro admixture (Nurse & Jenkins 1977).

The Gm system of serum protein polymorphisms appears to be one of the most useful so far discovered for the elucidation of anthropological problems in southern Africa (Nurse & Jenkins 1977). The $Gm^{1,5,6}$ haplotype appears to be characteristic of the Negro, and the $Gm^{1,13}$ (and to a lesser degree the $Gm^{1,21}$) haplotype is common amongst the San peoples, while $Gm^{1,13}$ is rare and $Gm^{1,21}$ is virtually absent in other sub-Saharan African populations (Jenkins & Steinberg 1966; Jenkins *et al.* 1970; Steinberg *et al.* 1975).

Only a few of the apparent genetic differences found so far among the San and Negro are mentioned above (see Tobias 1972; Nurse & Jenkins 1977). It appears that while some alleles are characteristically San (or Khoisan) (e.g. A^{bantu} , acid phosphatase Pr , Fy^a , $Gm^{1,13}$) others are characteristic of the Negro (e.g. peptidase Pep^{A2} , $Gm^{1,5,6}$). Furthermore, the frequency distributions of these various genes amongst the San and Negro populations seem to indicate a certain amount of genetic exchange between the two groups. The quantity of genetic exchange is difficult to ascertain because of uncertainties about the part played by drift or selection in the attainment of the frequencies of certain alleles in the San and Negro. For example, the transferrin D_1 variant, which is frequently found amongst the San and less commonly shown by the southern African Negro, has been shown to be electrophoretically and chemically

identical to that found among Australian aborigines (Krik *et al.* 1964; Wang *et al.* 1967). The San also manifest, in common with the Australian aborigines, low or absent frequencies of S in the MNSs Henshaw system and the occasional presence of adults with the Lewis Le (a+b+) phenotype (Nurse & Jenkins 1977). These similarities may reflect parallel adaptations to the selective pressures imposed by similar environments and modes of life.

How do the results obtained from the present study of the occlusal morphology of the permanent lower molars of the San and the South African Negro compare with the results of other morphological and genetic studies on these people?

Comparative data on the principal cusp numbers, the primary occlusal patterns, the tuberculum sextum and tuberculum intermedium for other African and New World Negro populations have been recorded (see Tables 4-6, 8-14, 19, 21). Data for the frequencies of the tuberculum sextum and tuberculum intermedium are available for relatively few non-South African Negro populations. The South African Negro frequencies for the tuberculum sextum on all three molars fall within the frequency ranges for other Negro populations (Table 19) and the South African Negro frequencies for the tuberculum intermedium on the first and third molars fall between the frequencies shown by the west African and American Negro populations. The South African Negro very rarely shows a tuberculum intermedium on the second molar; this frequency is lower than that of any other Negro population and closely approximates the San incidence (Table 21).

Considerably more comparative Negro data are available for principal cusp number and primary occlusal pattern frequencies. The frequency of five-cusped first mandibular molars in the South African Negro is amongst the highest recorded for Negro populations and closely approximates the San frequency (Table 4). Although the incidence of five-cusped second permanent molars in the South African Negro (47,6 per cent) is significantly lower than the San incidence (78,4 per cent), frequency for the South African Negro is considerably higher than for any other Negro population so far examined (Table 5). It is possible that the relatively high frequency of five-cusped second molars in the South African Negro is due to a certain amount of San admixture. Similarly, the San and South African Negro show comparatively high frequencies of five-cusped third mandibular molars. Only Hellman's (1928) west African population shows an incidence comparable with that of the South African Negro (Table 6).

On the other hand, the South African Negro possesses the lowest frequency of the Y pattern on the first molar of any Negro population so far studied (Tables 9-10). The San shows a higher (albeit insignificantly so) incidence of this pattern than the South African Negro on the first mandibular molar, and the San incidence is thus closer to those shown by non-South African Negroes than it is to the South African Negro frequency. Similarly, the South African Negro shows a significantly lower frequency of the Y pattern on the second

mandibular molar than does the San, and the incidences of almost all other Negro populations are higher than that of the South African Negro and thus closer to the San frequency (Tables 11–12).

Thus, in certain features of the lower molars (e.g. principal cusp number, and perhaps, the tuberculum intermedium on the M_2) the San and South African Negro seem to display frequencies that are more similar to each other than either is to most non-southern African Negroes. And this is evident despite the fact that in some of these instances (e.g. principal cusp number on the M_2) the San and South African Negro frequencies are significantly different. In other characters (e.g. the primary occlusal pattern), however, the South African Negro frequencies appear to be further removed from those of the San than the incidences shown by other Negro populations.

As discussed previously for each character, the San and other African (Negro) populations generally show frequencies more in common compared with the differences that separate Subsaharan Africans from most other racial constellations.

Thus, the results of the present study on the mandibular molar morphology of the San and South African Negro are compatible with, and to some degree corroborate, the conclusions reached by others who have examined gross morphological and gentic features of these peoples (e.g. De Villiers 1968; Rightmire 1970; Tobias 1972; Nurse & Jenkins 1977). Although there is evidence that at least some dental features are monogenic, the modification by environmental factors of the genetic control over the expression of these dental traits and the degree to which these variants are selectively affected by wear and disease are far from completely understood. Because of these problems, Berry (1976) has questioned the practical value of minor crown variants in anthropological studies. Nevertheless, when used in conjunction with the results of studies on other gross morphological features and the results of genetic studies on the people in question, dental traits seem to convey information as reliable as that gained from other, non-dental characters.

Perhaps the most serious drawback to the anthropological usefulness of dental traits is the question of the usefulness, for comparative purposes, of data published by different workers in view of the inter-observer differences in the scoring of dental variants.

SUMMARY

A series of morphological characters of the permanent mandibular molars of the South African Negro and Kalahari San have been investigated. These features include the principal cusp number, the presence or absence of the tuberculum sextum and tuberculum intermedium, the form of the primary occlusal pattern, the presence or absence of a deflecting wrinkle and the mesial and distal foveae, and the appearance of the occlusal enamel. The definitions and various methods employed in the classification of these characters are reviewed.

Significant sexual dimorphism in the morphology of the mandibular molars is relatively low in both the San and Negro. Such dimorphism is expressed variously by these populations in only three of the eight features examined (i.e. the deflecting wrinkle, the fovea anterior and the presence of crenulate enamel), and even then sexual dimorphism is not expressed on all three molars for these three features.

While there is a low incidence and degree of sexual dimorphism in the features examined, significant populational differences amongst the San and Negro are more common. The fovea anterior and the tuberculum sextum appear to be respectively the first and second most useful discriminatory characters, while the second molar displays the greatest number of significant differences between the San and the Negro. A characterization of the lower molar morphology of the San and Negro is provided.

Paired chi-square evaluations of interdependence have been performed for most of the characters examined. Most of the features were found to be independent of one another. Principal cusp number and primary occlusal pattern appear to have a sometimes low level of dependence in the Negro, but in most instances these two characters seem to be independent. No relationship is evident between the presence of a deflecting wrinkle and the presence of a Y occlusal pattern.

The biological differences and similarities of the San and Negro as determined by both gross morphological and genetic studies are reviewed. A number of morphological and genetic features that may be considered characteristic of the San are found in varying frequencies in South African Negro populations. It is generally assumed that 'hybridization' has brought some of the 'San alleles' into the gene pool of the southern African Negro. Furthermore, it is postulated by most workers that these San characteristics were acquired secondarily by the Negro in the course of their southward migrations. In certain of the dental features examined here the San and South African Negro frequencies appear to be more similar to one another compared with frequencies shown by other Negro populations. Thus, the dental data presented here for the San and South African Negro are compatible with, and to some degree corroborate, what is known about the interrelationships of these peoples from non-dental morphological and genetic data.

Perhaps the most serious drawback to the anthropological usefulness of dental traits is the question of the comparative usefulness of data published by different workers in view of the inter-observer differences in scoring these traits.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Capital initial letters

- (a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
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Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

F. E. GRINE

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OF THE MANDIBULAR PERMANENT MOLARS
OF THE SOUTH AFRICAN NEGRO AND
THE KALAHARI SAN (BUSHMAN)

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A HYENA-ACCUMULATED BONE
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DEPOSITS AT DEELPAN, ORANGE FREE STATE

By

L. SCOTT

&

R. G. KLEIN

Cape Town Kaapstad

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A HYENA-ACCUMULATED BONE ASSEMBLAGE FROM LATE HOLOCENE DEPOSITS AT DEELPAN, ORANGE FREE STATE

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University of the Orange Free State*

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(With 3 figures and 2 tables)

[MS accepted 5 August 1981]

ABSTRACT

Late Holocene sands fringing Deelpan, Western Orange Free State, have yielded a sample of bones derived from steenbok, springbok, black wildebeest, blesbok, quagga or Burchell's zebra, caracal or serval, slender mongoose, clawless otter, black-backed jackal, and eagle or hawk, as well as coprolites of a hyena. The composition of the fauna is in keeping with pollen evidence that highveld vegetation prevailed at the time the bones accumulated. The absence of artefacts and porcupine gnaw marks, in combination with the hyena coprolites and two bones almost certainly damaged by hyena teeth, indicate that hyenas were responsible for the bone accumulation. Like other hyena-accumulated samples, the Deelpan one differs from human (archaeological) samples in the relatively high number of carnivore individuals represented and in the tendency for the ratio of postcranial to cranial bones to increase with the size of the species involved.

CONTENTS

	PAGE
Introduction.....	217
Setting	218
Context of the bone assemblage.....	219
The bone assemblage.....	220
Acknowledgements	226
References.....	226

INTRODUCTION

In the course of a multidisciplinary investigation into the history and origin of pans in the Orange Free State, Scott recovered an assemblage of bones from unconsolidated sandy deposits on the eastern margin of Deelpan (Honing Kopje Pan) (approximately 29°11'S 25°45'E), between Bloemfontein and Petrusburg (Fig. 1). Artefacts were absent, and nine associated coprolites, together with damage marks on two of the bones, point to hyenas as the bone collectors. In this brief report, Scott describes the setting and sedimentary

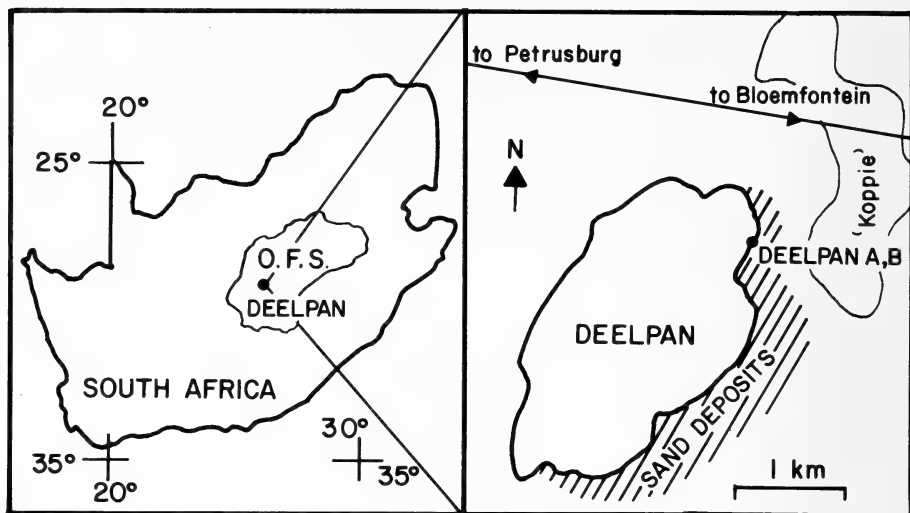


Fig. 1. *Left:* The location of the Deelpan fossil site within South Africa. *Right:* A schematic plan of Deelpan, showing the distribution of the sandy deposits on its southern and eastern margins and the points (Deelpan A and B) where bones were recovered.

context of the bone assemblage, while Klein discusses its implications for distinguishing hyena bone accumulations from human (archaeological) ones. In a future paper, K. W. Butzer (University of Chicago) will analyse a suite of sediment samples from the site, with the goal of elucidating its climatic and environmental history.

SETTING

Deelpan is typical of the numerous pans or playas that dot the plains of the western Orange Free State (De Bruijn 1971, 1972; Le Roux 1978). The pans are thought to result from the interaction of bedrock geology, slope, salt concentration, chemical weathering, seasonal climate, and animal activity, the combined effect of which is to foster deflation. The prevailing westerly winds then build sand-dunes along the south-eastern and eastern margins of most pans in the region (De Bruijn 1971, 1972).

The open plains of the Orange Free State are underlain by typical Karoo sedimentary rocks intruded by dolerites that form rocky hills ('koppies'). Annual precipitation in the Deelpan area is less than 500 mm. The vegetation belongs to the so-called False Upper Karoo (Acocks 1953, veld type 36), comprising grassland with a high proportion of Karoo shrubs, especially Compositae. Woody species such as *Olea africana*, *Rhus lancea*, and *Rhus erosa* occur on dolerite 'koppies'. The pan floor of approximately 6.5 km² does not support any vegetation and consists of clays rich in carbonates and other salts

concentrated on the surface through evaporation. During most of the year, the pan is dry, except for the south-western portion where perennial springs occur. However, during especially rainy years, water may fill the pan to a depth of 2 m and remain for a year or more. When filled, the pan attracts countless numbers of water-birds. In prehistoric times, it probably also attracted large numbers of antelopes and other animals. Artefacts found along the margins of Deelpan and various other pans in the region point to frequent visits by prehistoric man (Butzer *et al.* 1973; Butzer 1974; Horowitz *et al.* 1978).

CONTEXT OF THE BONE ASSEMBLAGE

As at many western Free State pans, unconsolidated Quaternary deposits at Deelpan occur along its southern and eastern margins. Recent erosion of these deposits has allowed recognition of a three-part sedimentary sequence (from top to bottom): 1, more than 2 m of semi-compacted sands, exhibiting distinct stratification in places; 2, approximately 1 m of semi-compacted, non-stratified sands, especially obvious in the southernmost exposures; and 3, more than 3 m of compact, calcareous clayey sands. The bones described here came from near the bottom of the uppermost unit (1). Only traces of bones were found in the two lower units, along with occasional mollusc shells and fragments of ostrich egg-shell.

Within the uppermost sedimentary unit, bones were found at the same level in two distinct concentrations, labelled A and B, approximately 3 m apart. At point B, a subtle colour difference suggests the bones lie in a pocket roughly 30 cm across within the loose sands. It seems likely that the pocket is the cross-section of an ancient burrow, quite possibly part of a system also including the bone occurrence at A. This hypothesis can be checked only by excavation, which may also lead to the recovery of bones in the sands between A and B. The present bone collection consists totally of pieces that were eroding out of the sections at A and B or had already eroded out and were lying on the pediment below.

Preliminary observations indicate that the sedimentary sequence observed at Deelpan also characterizes the unconsolidated sediments found at most isolated pans in the western Orange Free State. The similarity almost certainly reflects a common response to past climatic change. Horowitz *et al.* (1978) have described an especially similar sequence at Voigtspost Pan, approximately 40 km west of Deelpan. The specific palaeoclimatic events involved at Voigtspost remain to be worked out, but comparison to Deelpan is still informative. Particularly pertinent are ^{14}C determinations of 6350 ± 75 B.P. (Pta - 1520) and 1220 ± 50 B.P. (Pta - 1483) on ostrich egg-shell fragments from sediments at Voigtspost equivalent to Deelpan sedimentary units 3 and 1 respectively. The dates indicate that the visible sedimentary sequences at Voigtspost and Deelpan date from the Holocene, while the bone assemblage from Deelpan A and B is probably of late Holocene age.

Limited palynological evidence from Voigtspost suggests that the middle unit (equivalent to unit 2 at Deelpa) was deposited under slightly moister conditions than the underlying and overlying sediments (equivalent to units 3 and 1 at Deelpa). However, the pollen spectra imply basically highveld vegetation throughout the sequence. The pollen from the uppermost sands at Voigtspost, equivalent to the bone-bearing unit at Deelpa, comprises 2% Gramineae, 43% Chenopodiaceae, 11% Compositae, 30% spores of *Riccia* and *Ophioglossum*, and traces of other plants. Pollens were not found in the equivalent Deelpa sediments, but 90% of the pollen found in coprolites accompanying the Deelpa bones derived from Gramineae. The difference probably reflects the differing nature of sediments and coprolites as pollen traps, plus the fact that the pollen in the Voigtspost samples was probably deposited over a relatively long period in the halophytic environment of the pan shore. Like the Voigtspost pollen, that in the Deelpa coprolites almost certainly reflects essentially highveld vegetation.

THE BONE ASSEMBLAGE

Since there is every likelihood that the bones from Deelpa A and B were accumulated at the same time by the same agency, they have been treated here as a single assemblage. The bones are relatively fresh looking, with no apparent mineralization, in keeping with their probable late Holocene age. Fragmentation is minimal and nearly every piece was immediately identifiable to skeletal part and species.

The species represented are listed in Table 1, which also presents the number of bones assigned to each and the minimum number of individuals from which the bones derive. The skeletal parts by which each species is represented are listed in Table 2. The ungulate species present are the classic, historic inhabitants of the highveld, and their occurrence is thus totally in keeping with pollen evidence that highveld vegetation prevailed at the time the

TABLE 1

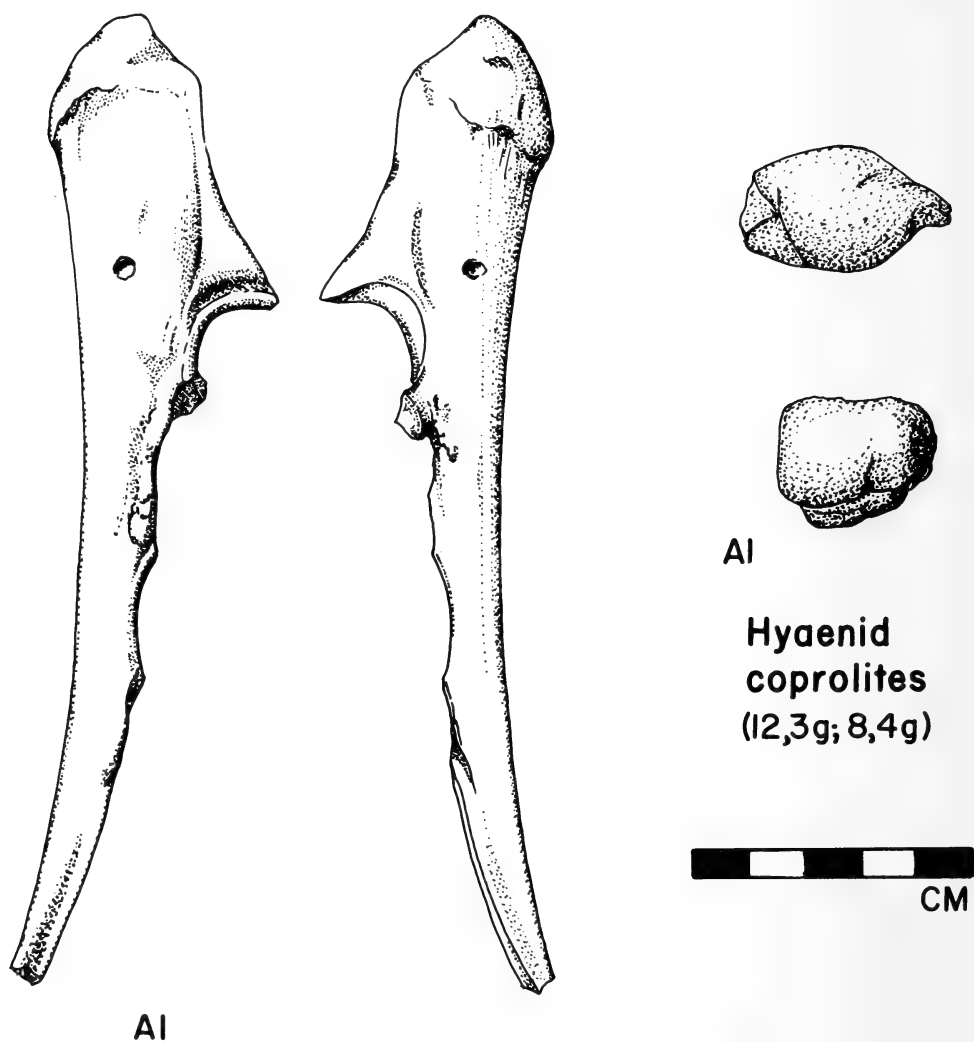
The number of identifiable bones; the minimum number of individuals by which various species are represented in the bone assemblage from Deelpa A and B.

steenbok (<i>Raphicerus campestris</i>)	1/1
springbok (<i>Antidorcas marsupialis</i>)	48/3
black wildebeest (<i>Connochaetes gnou</i>)	24/4
blesbok (<i>Damaliscus dorcas</i>)	11/2
quagga or Burchell's zebra (<i>Equus quagga</i> or <i>E. burchelli</i>)	1/1
caracal or serval (<i>Felis caracal</i> or <i>F. serval</i>)	3/1
hyena (Hyaenidae gen. et sp. indet.)	9 coprolites
slender mongoose (<i>Herpestes sanguineus</i>)	1/1
clawless otter (<i>Aonyx capensis</i>)	2/1
black-backed jackal (<i>Canis mesomelas</i>)	6/2
eagle or hawk (Accipitridae gen. et sp. indet.)	2/1

TABLE 2
The number of identifiable bones/the minimum number of individuals per skeletal element per taxon in the fauna from Deelpan A and B.

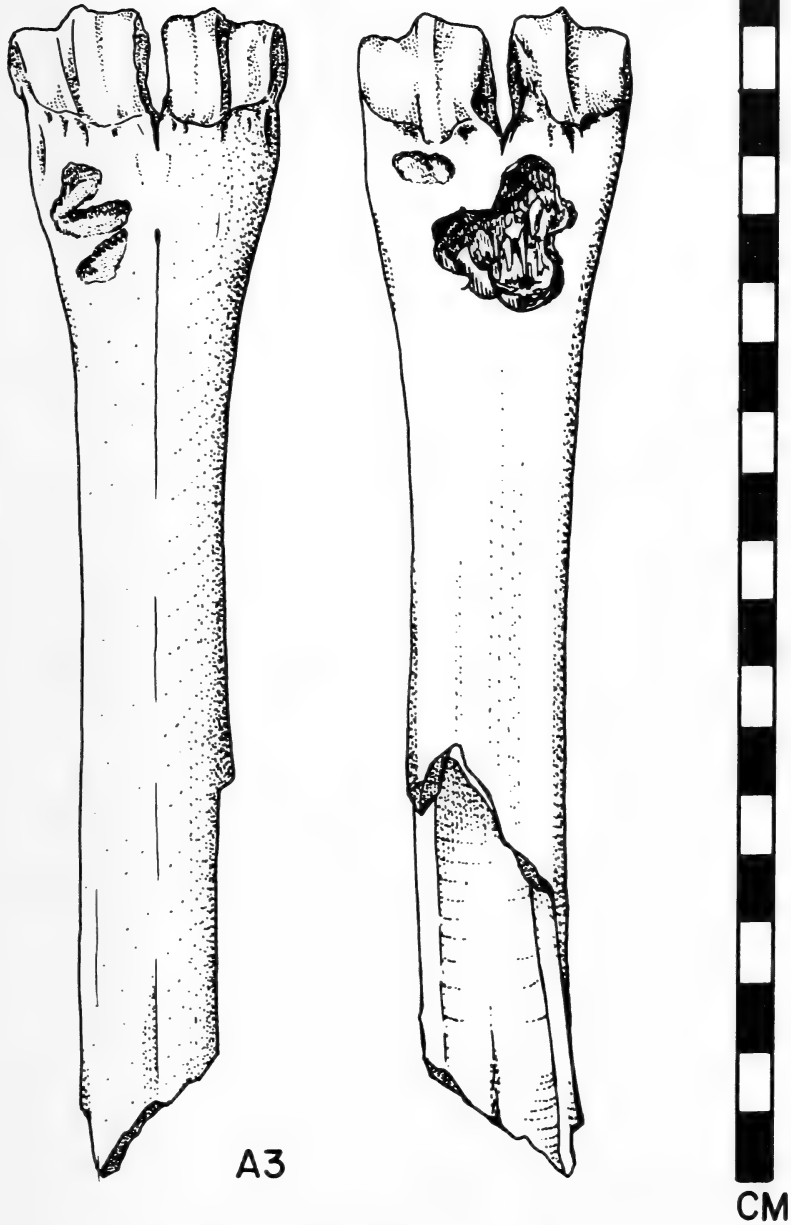
	steenbok	springbok	wildebeest	blesbok	quagga/ zebra	caracal/ serval	mongoose	otter	jackal	eagle/ hawk
frontlet										
male		2/2								
female		1/1		1/1						
maxilla		3/2		2/1						
mandible		4/2		1/1				2/1	2/2	
atlas		1/1	1/1							
axis		1/1	2/2							
other cervicals		4/1	2/1			2/1				1/1
thoracic vertebrae		1/1								
lumbar vertebrae										
sacral vertebrae										
caudal vertebrae		2/1								
ribs		4/1								
scapula		3/2	1/1							
humerus		2/2	3/3						1/1	1/1
radius		4/2	3/2	2/2			1/1			
ulna		1/1		1/1						
carpals		1/1	1/1							
metacarpals		5/2	4/4	2/2		1/1				
innominate	1/1	1/1	1/1							
femur		1/1								
tibia		3/2	1/1							
patella										
astragalus		1/1	1/1							
calcaneum			1/1							
other tarsals			2/1						1/1	
metatarsals		1/1			1/1					
phalanges		3/1	1/1	1/1						

bones accumulated. The species composition is also totally consistent with a late Holocene age. The complete absence of domestic stock (cattle and/or sheep and goats) further suggests that the bones antedate European settlement of the area, beginning in the middle part of the last century. It is possible that domestic stock were introduced to the area even earlier by indigenous Khoi



Damaliscus dorcas

Fig. 2. *Left:* A blesbok ulna from Deelpan A displaying punctate depressions probably caused by the canines of a hyena. *Right:* Hyena coprolites from Deelpan A.



Connochaetes gnou

DEELPAN

Fig. 3. A black wildebeest distal metacarpal from Deelpan A exhibiting damage to the outer table that was probably caused by hyena chewing.

herders or Iron Age mixed farmers, but Deelpan lies in a relatively dry region where both archaeological and historic records suggest that prehistoric occupation was largely, if not exclusively limited to hunter-gatherers (Maggs 1976).

In southern Africa, there are three potential accumulators of bones at a site such as Deelpan. Two—people and porcupines (*Hystrix africaeaustralis*)—are ruled out by the absence of their telltale signs—artefacts and gnaw marks respectively. The third—hyenas—are clearly indicated by the presence of their coprolites (9 in total) and of two ungulate bones with what are almost certainly damage marks from carnivore teeth (Figs 2–3).

Both the brown hyena (*Hyaena brunnea*) and the spotted hyena (*Crocuta crocuta*) occurred in the region of Deelpan historically, and both are known to accumulate bones in dens or lairs, including abandoned aardvark burrows or other subterranean cavities of sufficient size. It is such burrows, now filled in or collapsed, that may well be represented at Deelpan. The brown form is the more prodigious bone collector of the two, largely because it brings food back to its young, while the spotted form does not. The two species also differ in the kinds of animals that they most frequently eat. The brown hyena feeds much more often on species springbok-size and smaller, reflecting its general incompetence as a hunter and its inability to retain the carcasses of larger animals when other large predators—scavengers are also present. (See Sutcliffe (1970), Kruuk (1972), Bearder (1977), Mills (1978a), Mills & Mills (1977), and Henschel *et al.* (1979) for information on the spotted hyena; Mills (1973, 1978b), Mills & Mills (1977), Skinner (1976), and Owens & Owens (1978, 1979) for data on the brown hyena.)

Tables 1 and 2 show that springbok is the most common species at Deelpan in terms of the number of identifiable bones, while black wildebeest is most common in terms of the minimum number of individuals represented. In combination with the fact that the relative abundance of these species in the ancient Deelpan environment remains unknown and perhaps unknowable, this means that the species frequencies in the present sample do not help to establish which hyena accumulated the bones. Perhaps ultimately this question will be resolved, if it becomes possible to identify the coprolites to species.

Whichever hyena is responsible, the Deelpan assemblage contrasts with hominid (archaeological) bone assemblages in two important respects:

1. The relative abundance of carnivores. In minimum individual terms, carnivores constitute 31% of the animals in the Deelpan sample, while there is no archaeological sample in Africa in which the comparable figure has been found to exceed 13%. The contrast probably reflects the fact that hyenas (especially the brown species) interact with other carnivores (especially jackals) much more frequently than hunter-gatherers do.

2. At Deelpan, there is a clear tendency for larger species to be relatively better represented by postcranial bones than by cranial ones. In archaeological assemblages, there is no such trend, and the cranial:postcranial ratio does not seem to be related to the size of the species concerned. The contrast probably

reflects the fact that hyenas find it far more difficult to transport the skulls of large animals than people do, while both kinds of bone accumulators find postcranial bones about equally portable.

Klein has found that the same features characterize fossil bone assemblages collected by hyenas at other sites in southern Africa, particularly Swartklip 1 (Hendey & Hendey 1968; Klein 1975), Equus Cave (Beaumont & Shackley pers. comm.; Klein in preparation), and the Elandsfontein 'Bone Circle' (Inskeep & Hendey 1966; Klein unpub.). These other samples are all much larger than the Deelpan one, and the fact that the features are still clear at Deelpan is thus a measure of the strength of the pattern they represent.

One feature that might be expected to characterize hyena accumulations would be a large number of bones obviously damaged by the animals' teeth. In fact, such bones are relatively rare not only at Deelpan but also in the other fossil assemblages mentioned above and apparently in assemblages from dens where living hyenas were observed, though precise figures on damaged bones from such dens are generally lacking. (The bones found at active dens are discussed in some of the papers on hyena feeding and foraging cited above.) The implication of this is that, where there is doubt as to the human or hyenid origin of a particular bone assemblage, principal reliance will probably have to be placed on relatively subtle features such as the abundance of carnivores or the nature of the relationship between species size and cranial:postcranial bone representation.

In southern Africa, the most important bone assemblages whose origins remain problematic are certainly those from the various australopithecine caves in the Transvaal. The question is basically whether the bones were brought to the caves by the australopithecines, as argued particularly by Dart (1957a, 1957b) or perhaps by a carnivore, as discussed particularly by Brain (1980, 1981). *A priori*, in considering the possibility that hyenas were involved, it might seem most reasonable to attack the problem by analysing bones from recent hyena dens. However, the samples from such dens tend to be very small, while the dens themselves are mostly in marginal or degraded environments. Often, many of the bones present come from domesticated species. Furthermore, especially in the case of the brown hyena, which has become comparatively rare, it is unlikely that there are very many dens left to be sampled. All this means that the study of the fossil collections is essential both to establish a convincing pattern of differences between hyena and hominid assemblages and to maintain reasonable control over environmental and ecological variables in exploring the origins of assemblages such as those from the australopithecine caves.

Klein (1975) has already argued that there are marked similarities between the bone assemblage from Swartklip (and by extension from Deelpan and other hyena-accumulated samples) on the one hand and the bone assemblage from Makapansgat on the other, as partially described by Dart (1957a, 1957b) and Wells & Cooke (1956). Some fresh data on the Makapansgat carnivores

presented by Collings *et al.* (1975) suggest, in fact, that the bone accumulation at Makapansgat, at least from the so-called 'Grey Breccia' (Member 3 of Partridge 1979), probably owes its origin largely, if not entirely, to the ancestral striped hyena, *Hyaena hyaena makapani*. Ultimately, it should prove possible to reach reasonable closure on this issue through the analysis of more assemblages such as the one from Deelpan and through more detailed study of the Makapansgat collection.

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Nuculana (Lembulus) bicuspidata (Gould, 1845)
Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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Holotype

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L. SCOTT
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RELATIVE SIZES OF THE
MAXILLARY DECIDUOUS CANINE AND
CENTRAL INCISOR TEETH
IN THE KALAHARI SAN (BUSHMAN)
AND SOUTH AFRICAN NEGRO

By

F. E. GRINE

Cape Town Kaapstad

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AND SOUTH AFRICAN NEGRO

By

F. E. GRINE

South African Museum, Cape Town

(With 1 figure and 9 tables)

[MS accepted 26 August 1981]

ABSTRACT

The mean canine-incisor index of the San is low (i.e. the San tend to possess relatively small canines), while the average Negro index is high. The Negro mean index value is rather high compared to values computed for other human groups, while the San index is one of the lowest recorded for any population. The canine-incisor index, in conjunction with other dental and osteological features, may prove to be useful in the identification of human (particularly immature) remains from African, and especially southern African, archaeological sites.

CONTENTS

	PAGE
Introduction	229
Material	230
Methods	231
Results	232
Discussion	240
Summary	242
Acknowledgements . .	243
References	243

INTRODUCTION

In the course of a study of the milk teeth of Japanese and American populations and their offspring, Hanihara (1955) noted a difference in the relative sizes of the maxillary deciduous canines among Japanese, 'Japanese-American White hybrid' and 'Japanese-American Negro hybrid' samples. With the accumulation of more comparative material, Hanihara (1966) later proposed the relative size of the upper milk canine to be a racial character of the dentition. He compared the size of the maxillary deciduous canine (d^c) with that of the maxillary deciduous central incisor (di^1) to compute what he termed the 'canine breadth index'. This index was calculated by the simple formula:

$$I = \frac{MD\ d^c}{MD\ di^1} \times 100$$

where $MD\ d^c$ is the mesiodistal diameter of the canine and $MD\ di^1$ is the corresponding dimension of the incisor. Hanihara observed that in most Caucasoid population samples the mean index value exceeded 105.0 per cent,

while in other groups (e.g. Mongoloid, Negroid, and Australoid) the average index had a value of around 100,0 per cent. A relatively high 'canine breadth index' was considered by Hanihara (1967, 1968, 1970) to constitute part of what he called the 'Caucasoid dental complex' including also several other features such as a high frequency of the Carabelli trait on the dm^2 and a low frequency of incisor shovelling.

Although Hanihara (1955, 1966, 1967, 1968, 1970) directly recorded indices and calculated average index values from previously published dimensional data for several different racial samples, no data are at present available for southern African Negro and Khoisan populations save for the tooth dimensions recorded by Abel (1933). Hanihara (1966: table 5) computed an index from Abel's data and considered this index as a value for the 'Bantu'. However, Abel's data are derived from a mixed sample of Khoi (Hottentot), San (Bushman), and Negro crania, and as such these data are not representative of a homogenous population. (The term 'Bantu' refers to the family of languages spoken by southern African Negro peoples and not to a biological group, although the term is often used erroneously in biological contexts.) The present paper records this index of relative d^c size for the South African Negro and Kalahari San derived from the author's unpublished dental measurements on samples drawn from these populations.

Note should be made of the term 'breadth' as used by Hanihara (1966) in his 'canine breadth index'. The term 'breadth' has been used by various authors in reference to either the mesiodistal or the buccolingual (=labiolingual) diameters of tooth crowns (see Moorrees 1957, Tobias 1967, and Lunt 1969 for complete discussions of this terminological problem). In order to avoid confusion by the use of the term 'breadth' in reference to an index calculated from mesiodistal diameters, Hanihara's 'canine breadth index' is probably better referred to by another name. In this paper it will be referred to as the 'mesiodistal canine-incisor index'.

MATERIAL

The material examined in this study is drawn from the Khoisan and Negro population groups of southern Africa. The Negro sample comprises crania of South African Bantu-speaking Negroes housed in the Raymond A. Dart Collection of Human Skeletons, Department of Anatomy, University of the Witwatersrand, Johannesburg, and also by plaster casts made from the impressions of the teeth and dental arches of living Natal Nguni children. Because of the high incidences of damaged, lost, and diseased teeth in the available Negro samples, only six male and six female subjects were found in which both the di^1 and d^c could be measured.

The term 'San' is used in this study to denote a biological population, whereas the name 'Bushman' refers more precisely to the ethnological and linguistic practices of these peoples (Jenkins & Tobias 1977). The San sample

is composed entirely of plaster casts made from the impressions of the teeth and jaws of living subjects. The casts were made by J. F. van Reenen and his co-workers on three expeditions to the Kalahari Desert in 1958, 1959, and 1964. Both the di^1 and d^c were measurable on some thirty-four male and twenty-four female specimens.

METHODS

To measure the diameters of the teeth a sliding vernier caliper equipped with a dial was used. The points of the caliper were tapered and sharpened in order to enable them to be inserted into the interdental embrasures between teeth in the jaw. The mesiodistal crown diameters of the di^1 and d^c were recorded to the nearest 0.1 mm.

Several different methods have been defined and used in the measurement of mesiodistal crown diameter (Hrdlička 1923; Campbell 1925; Martin 1928; Remane 1930; Shaw 1931; Pedersen 1949; Selmer-Olsen 1949; Robinson 1956; Moorrees 1957; Korenhof 1960; Goose 1963; Jacobson 1967; Tobias 1967; Lunt 1969). The determination of the mesiodistal diameters of the di^1 and d^c employed here was made according to Tobias's (1967) definition of this dimension. That is, the mesiodistal diameter was measured as the distance between two parallel lines perpendicular to the mesiodistal axial plane of the tooth and tangential to the most mesial and distal points of the crown. Moreover these points lay along a line parallel to the occlusal plane. This measurement is, accordingly, not dependent upon the position of the tooth in the dental arch and the termini do not necessarily correspond to the points of interstitial contact.

Interproximal attrition may have an appreciable effect on the mesiodistal diameter of a tooth crown. In those instances where attritional reduction of tooth material was slight, and the amount of loss could be estimated with a reasonable degree of accuracy, the mesiodistal measurement was corrected so that it approximated the unworn diameter. For teeth that were heavily worn, and for which mensurable correction was more a 'guesstimate' than a reasonable estimate, a dimension was not recorded.

The mesiodistal diameters of the di^1 and d^c were recorded and the canine-incisor index was calculated separately for each individual according to the formula given above. Only a single incisor and a single canine (usually the left) were measured for each individual. The data was processed by a shortened version of the OSIRIS programme, and the computation of statistics was performed using the SPSS programmes package (Nie *et al.* 1975).

Except for the indices recorded by Hanihara for sexually pooled samples of Japanese, Amerindians (Pima), Alaskan Eskimos, American Caucasoids, American Negroes, 'Japanese-American White hybrids' and 'Japanese-American Negro hybrids' (1966: table 2), all the indices for comparative populations used in this paper were calculated from reported means of mesio-

distal diameters of the di^1 and d^c . It should be noted that a *mean index* and an *index of means* computed for a single population sample will not necessarily be the same. For example, the canine-incisor index of San males calculated as an average of individual indicial values (a *mean index*) is 97,8 per cent (Table 1), while the index computed from the mean di^1 and d^c dimensions (an *index of means*) is some 98,2 per cent (Table 3). Nevertheless, the different values obtained by these two methods of calculation appear to be similar enough to permit comparison of the present results with the indices computed from the mean crown diameters recorded for other population groups.

RESULTS

The canine-incisor indices obtained for the Kalahari San and South African Negro samples are recorded in Table 1. It is immediately apparent that on average the San possesses a relatively smaller maxillary deciduous canine

TABLE 1

Canine-incisor indices of the Kalahari San and South African Negro.

<i>Population sample</i>	N	\bar{X}	SE	SD	CV	<i>Sample range</i>
San male	34	97,81	1,05	6,09	6,23	90,0–113,3
San female	24	97,95	1,16	5,69	5,81	89,2–109,5
San male + female	58	97,87	0,77	5,88	6,01	89,2–113,3
Negro male	6	107,03	3,26	7,98	7,46	100,0–122,4
Negro female	6	102,90	3,12	7,65	7,43	91,6–113,6
Negro male + female	12	104,97	2,24	7,76	7,39	91,6–122,4

N—sample size; \bar{X} —sample mean; SE—standard error of the mean;

SD—standard deviation; CV—coefficient of variation ($SD/\bar{X}(100)$).

than does the South African Negro. All San sample means fall below 100,0 per cent, while all Negro means fall above 100,0 per cent. Individual index values for all samples, except the Negro male, range from below to above 100,0 per cent.

Despite the small sizes of the Negro male and female samples, F analyses of variance revealed no apparent significant differences in the index value distributions amongst these and the other samples considered here. Statistical testing of the means of the various samples, notwithstanding the small sizes of some, was considered justified. The results of these comparisons are given in Table 2.

The mean index values of the San male and female samples are nearly the same (Table 1) and, as expected, this slight difference was found to be not statistically significant. The mean index value of the Negro male sample is somewhat higher than that of the Negro female sample (Table 1), but this mean difference was also found to be not statistically significant. Thus no apparent sexual differences are shown by the San and Negro samples in the

TABLE 2

Statistical comparison of mean canine-incisor index values amongst the Kalahari San and South African Negro samples.

<i>Sample comparisons</i>	<i>'t'</i>	<i>df</i>	<i>Significance</i>
San male—San female . . .	—0,09	56	—
Negro male—Negro female . .	0,92	10	—
San male—Negro male . . .	—3,27	38	p < 0,005
San female—Negro female . .	—1,78	28	—
San—Negro (pooled samples) .	—3,50	66	p < 0,001

df—degrees of freedom.

TABLE 3

Canine-incisor indices computed for different populations. Males.

<i>Population</i>	<i>MD di¹</i> (mm)	<i>MD d^c</i> (mm)	<i>Index</i> %	<i>Reference</i>
MONGOLOID				
Japanese	6,63	6,75	101,8	Ono 1960
Japanese	6,70	6,70	100,0	Hanihara 1976
Amerindian (Pima)	6,86	7,15	104,2	Hanihara 1976
CAUCASOID				
Rumanian	6,72	6,99	104,0	Boboc 1965
British	6,46	6,78	105,0	Clinch 1963
Swedish	6,60	7,04	106,7	Seipel 1946
North American	6,40	6,76	105,9	Black 1978
North American	6,40	6,80	106,3	Hanihara 1976
North American	6,55	6,88	105,0	Moorrees 1959
North American	6,46	6,81	105,4	Meredith & Knott 1968
AUSTRALOID				
Australian Aborigine . . .	7,35	7,41	100,8	Margetts & Brown 1978
Australian Aborigine . . .	7,40	7,52	101,6	Barrett, Brown & Luke 1963
Australian Aborigine . . .	7,31	7,35	100,6	Hanihara 1976
Naisoi	6,82	6,75	99,0	Bailit, De Witt & Leigh 1968
NEGROID				
American Negro	6,03	6,86	113,8	Hanihara 1976
South African Negro . . .			107,0	Present study†
South African Negro . . .	6,47	7,08	109,4	Grine unpublished††
KHOISANOID				
Kalahari San			97,8	Present study†
Kalahari San	6,78	6,66	98,2	Grine unpublished††
MIXED SAMPLE				
Tristanite	6,57	6,41	97,6	Thomsen 1955

†—mean of individual index values (mean index);

††—index calculated from mean dimensions of di¹ and d^c (index of means).

canine-incisor index. Hanihara (1955, 1966) found no significant sexual differences in the index values of any of the populations measured by him.

The Negro male displays, on average, a higher canine-incisor index than does the San male, and comparison of these mean values indicated this differ-

ence to be statistically significant (Table 2: 't' = -3,27; $p < 0,005$). The mean indicial value of the Negro female is higher than that of the San female; but comparison of these values indicated the difference to be not statistically significant, where a value of $p < 0,05$ was considered to represent significance. As would be expected from the foregoing the mean index value of the sexually pooled Negro sample is higher than the average value obtained for the pooled San sample (Table 1). Comparison of the pooled means (Table 2) indicated the Negro value to be significantly higher than that of the San ('t' = -3,50; $p < 0,001$).

The mean canine-incisor indices of the San and Negro male samples are compared with indices computed for male samples of other population groups in Table 3. It appears that while Caucasoid males display a relatively high index with values ranging from 104,0 to 106,7 per cent, Australoid males show a relatively low index with values ranging from 99,0 to 101,6 per cent. Males of the three Mongoloid populations recorded (Table 3) appear to show index values intermediate between the Australoid and Caucasoid values.

TABLE 4

Canine-incisor indices computed for different populations. Females.

<i>Population</i>	<i>MD di¹</i> (mm)	<i>MD d^c</i> (mm)	<i>Index</i> %	<i>Reference</i>
MONGOLOID				
Japanese	6,57	6,67	101,5	Ono 1960
Japanese	6,53	6,62	101,4	Hanihara 1976
Amerindian (Pima)	6,82	7,00	102,6	Hanihara 1976
CAUCASOID				
Rumanian	6,52	6,73	103,2	Boboc 1965
British	6,31	6,61	104,8	Clinch 1963
Swedish	6,56	6,93	105,6	Seipel 1946
North American	6,52	6,66	102,2	Black 1978
North American	6,40	6,76	105,6	Hanihara 1976
North American	6,44	6,67	103,6	Moorrees 1959
North American	6,32	6,73	106,5	Meredith & Knott 1968
AUSTRALOID				
Australian Aborigine	7,20	7,21	100,1	Margetts & Brown 1978
Australian Aborigine	7,29	7,31	100,3	Barrett, Brown & Luke 1963
Australian Aborigine	7,28	7,29	100,1	Hanihara 1976
Naisoi	6,71	6,53	97,3	Bailit, De Witt & Leigh 1968
NEGROID				
North American Negro	6,54	6,89	105,4	Hanihara 1976
South African Negro			102,9	Present study†
South African Negro	6,58	6,63	100,8	Grine unpublished††
KHOISANOID				
Kalahari San			98,0	Present study†
Kalahari San	6,70	6,49	96,9	Grine unpublished††
MIXED SAMPLE				
Tristanite	6,41	6,47	100,9	Thomsen 1955

† — mean of individual index values (mean index);

†† — index calculated from mean dimensions of di¹ and d^c (index of means).

Interestingly, the American Negro and South African Negro males possess the highest canine-incisor indices of any of the population groups compared, with values of 113,8 and 107,0 per cent (or 109,4 depending upon the mode of calculation) respectively. The index value of the San male, 97,8 per cent (or 98,2 depending upon the mode of calculation) is lower than that of any other male sample save the Tristanites.

Comparison of the mean index values recorded for the San and Negro female samples with the indices of means calculated for other female populations (Table 4) reveals a pattern of distribution similar to that described for males. The mean index of the South African Negro female (102,9%) falls within the range shown by Caucasoid female samples, whereas the South African Negro female index of means has a value of 100,8 per cent. The latter value is almost identical to that of the mixed Tristanite population, is lower than any Caucasoid or Mongoloid female value recorded, but is slightly larger than the values obtained for Australoid female samples. Only the Naisoi female index of means is lower than the mean index of the San female (98,0%), but the index value obtained from the mean tooth dimensions of the San female (96,9%) is lower than that recorded for any other population. Generally speaking, it appears that for most groups the mean female index value is somewhat lower than the average male index value.

The canine-incisor index of the sexually pooled South African Negro sample (105,0 or 104,3% depending upon the mode of calculation) is higher than that recorded for any Mongoloid or Australoid population, and falls within the ranges obtained for Caucasoids and established for other Negro populations (Table 5). The South African Negro index is considerably higher than that calculated for a sample of Liberian Negroes. It is also higher than the two index values recorded by Hanihara (1955, 1966) for 'Japanese-American Negro hybrids', and the index value calculated from Abel's (1933) data for a mixed sample of San, Khoi, and Negro individuals. The mean index, as well as the index of the means calculated for the South African Negro, are nearly the same as the mean index value recorded by Hanihara (1966, 1970) for the American Negro, but they are somewhat lower than the index values for American Negroes recorded elsewhere by Hanihara (1967) and computed from his 1976 data.

The San indicial value (either 97,9 or 97,6%) is lower than any recorded for a Caucasoid sample (Table 5). The San values are lower also than most obtained for Mongoloid populations, although they are approached by the values calculated for the Ainu (Hanihara 1970) and the Japanese sample measured by Arai (1937). The San values bracket the index value obtained by Hanihara (1955) for a Japanese sample. The San values are lower than those obtained for some Australoid populations, but are almost the same as the value calculated for the Naisoi, while the Australian Aboriginal index calculated from Campbell's (1925) data is lower. The Tristanite index value is also close to the San values. The San index values are lower than any recorded for a

TABLE 5

Canine-incisor indices reported or calculated for different populations.
Sexually pooled samples.

<i>Population</i>	<i>MD di¹</i> (mm)	<i>MD d^c</i> (mm)	<i>Index</i> %	<i>Reference</i>
MONGOLOID				
Japanese			97,7	Hanihara 1955
Japanese	6,60	6,71	101,7	Ono 1960*
Japanese	6,64	6,60	99,4	Arai 1937
Japanese			101,0	Hanihara 1966, 1970
Japanese			101,5	Hanihara 1967
Japanese	6,62	6,66	100,6	Hanihara 1976*
Ainu			99,5	Hanihara 1970
Amerindian (Pima)			103,3	Hanihara 1966, 1970
Amerindian (Pima)	6,84	7,08	103,5	Hanihara 1976
Amerindian (GKAH)	6,28	6,37	101,4	Sciulli 1977
Amerindian (PH)	6,42	6,44	100,3	Sciulli 1977
Alaskan Eskimo			100,3	Hanihara 1966, 1970
Aleut Eskimo			100,0	Hanihara 1966
CAUCASOID				
Rumanian	6,62	6,86	103,6	Boboc 1965*
Belgian medieval	6,33	6,85	108,2	Mydlarz 1964
European	6,10	6,70	109,8	Brabant 1965
Polish	6,40	6,90	107,8	Szlachetko 1959
British	6,30	6,60	104,8	Dolamore 1908
British	6,39	6,70	104,9	Clinch 1963
Swedish	6,58	6,99	106,2	Seipel 1946*
Aran Islander	6,30	6,80	107,9	Dockrell 1956
North American	6,50	7,00	107,7	Black 1897
North American	6,46	6,72	104,0	Black 1978*
North American	6,40	6,78	105,9	Hanihara 1976*
North American	6,50	6,90	106,2	Jones 1947
North American	6,50	6,78	104,3	Moorrees 1959*
North American	6,55	6,82	104,1	Kramer & Ireland 1959
North American			108,2	Hanihara 1966, 1970
North American			106,3	Hanihara 1967
North American	6,39	6,77	106,0	Meredith & Knott 1968
North American	6,40	6,80	106,3	Raak 1950
AUSTRALOID				
Australian Aborigine	7,28	7,31	100,4	Margetts & Brown 1978*
Australian Aborigine	7,35	7,42	101,0	Barrett, Brown & Luke 1963
Australian Aborigine	7,30	7,32	100,3	Hanihara 1976*
Australian Aborigine	7,80	7,50	96,2	Campbell 1925
Naisoi	6,77	6,64	98,1	Bailit, De Witt & Leigh 1968*
NEGROID				
American Negro			104,9	Hanihara 1966, 1970
American Negro			107,8	Hanihara 1967
American Negro	6,29	6,88	109,4	Hanihara 1976*
Liberian Negro	6,85	6,79	99,1	Moss & Chase 1966
South African Negro			105,0	Present study†
South African Negro	6,53	6,59	104,3	Grine unpublished††
KHOISANOID				
Kalahari San			97,9	Present study†
Kalahari San	6,75	6,59	97,6	Grine unpublished††

TABLE 5 (continued)

<i>Population</i>	MD di ¹ (mm)	MD d ^c (mm)	<i>Index</i> %	<i>Reference</i>
MIXED SAMPLES				
Japanese-Caucasoid . . .			102,2	Hanihara 1955
Japanese-Caucasoid . . .			102,4	Hanihara 1966
Japanese-Negro			99,5	Hanihara 1955
Japanese-Negro			101,0	Hanihara 1966
San-Khoi-Negro	6,60	6,60	100,0	Abel 1933
Tristanite	6,51	6,44	98,9	Thomsen 1955

In those instances where no MD diameters for di¹ and d^c are given, the index value was reported directly. *—index values calculated from averaged mean diameters of di¹ and d^c and are not the averages of male and female indices given in Tables 3 and 4. †—mean of individual index values (mean index); ††—index calculated from the mean dimensions of di¹ and d^c (index of means).

Negro population, although they are approximated by the values calculated for Liberian Negroes and a sample of 'Japanese-American Negro hybrids' examined by Hanihara (1955).

Thus the mean mesiodistal canine-incisor index value of the South African Negro appears to be relatively high, while that of the San seems to be relatively low compared with the values obtained for other human population samples.

Hanihara (1955, 1966) recorded the frequencies of individuals from several populations in whom the d^c was larger than the di¹ (index values equal to or greater than 100,1%) and in whom the d^c was smaller than or equal to the size of the di¹ (index values of x-100,0%). He (1966) recorded that the American Caucasoid sample had a higher frequency of individuals in whom the d^c was mesiodistally larger than the di¹ than did any of the other population samples examined by him.

The percentage frequencies of individuals with relatively small canines (index values of x-100,0%) and relatively large canines (index values of 100,1-x) in the South African Negro and San samples are recorded in Table 6. While no significant sexual differences in frequency distributions within the San and Negro samples were found (Table 7), it is readily apparent that, whereas the

TABLE 6

Numbers and frequencies of individuals in the South African Negro and Kalahari San samples in whom the deciduous canine is smaller than, and/or equal to, or larger than the central deciduous incisor.

<i>Population sample</i>	<i>Index value x-100,0%</i>		<i>Index value 100,1-x%</i>	
	N	% Frequency	N	% Frequency
San male	25	73,5	9	26,5
San female	17	70,8	7	29,2
San—male + female .	42	72,4	16	27,6
Negro male	1	16,7	5	83,3
Negro female	2	33,3	4	66,7
Negro—male + female	3	25,0	9	75,0

TABLE 7

Chi-square evaluation of distribution of index values above and below 100,0 per cent amongst the San and South African Negro.

<i>Sample comparisons</i>	χ^2	<i>significance</i>
San male—San female	0,05	—
Negro male—Negro female . .	0,44	—
San male—Negro male	7,25	$p < 0,01$
San female—Negro female . .	2,91	—
San—Negro (pooled samples) .	9,74	$p < 0,001$

TABLE 8

Comparison of frequencies of Kalahari San and South African Negro individuals with large or small canine-incisor indices with frequencies reported for other populations. Sexually pooled samples.

<i>Population</i>	<i>Index value $x-100,0$</i>		<i>Index value $100,1-x$</i>		<i>Reference</i>
	<i>N</i>	<i>% Frequency</i>	<i>N</i>	<i>% Frequency</i>	
Japanese	46	78,0	13	22,0	Hanihara 1955
Japanese	55	45,8	65	54,2	Hanihara 1966
Amerindian (Pima) . .	36	36,7	62	63,3	Hanihara 1966
Eskimo (Alaskan) . .	5	35,7	9	64,3	Hanihara 1966
American-Caucasoid .	2	11,1	16	88,9	Hanihara 1966
American Negro . . .	2	20,0	8	80,0	Hanihara 1966
South African Negro .	3	25,0	9	75,0	Present study
Kalahari San	42	72,4	16	27,6	Present study
Japanese-Caucasoid .	20	39,2	31	60,8	Hanihara 1955
Japanese-Negro . . .	12	48,0	13	52,0	Hanihara 1955

Numbers of individuals for other populations calculated from data presented by Hanihara (1966: table 4).

majority of San individuals have relatively small deciduous canines, the majority of Negro individuals have relatively large canines. Chi-square evaluations of the frequencies shown by the San and Negro samples revealed the difference between San and Negro males to be significant ($\chi^2 = 7,25$; $p < 0,01$), while the difference among the San and Negro females appeared to be not statistically significant. The distributional differences among the sexually pooled San and Negro samples were found to be highly significant ($\chi^2 = 9,74$; $p < 0,001$). While some 75,0 per cent of Negro individuals examined have maxillary deciduous canines that are mesiodistally larger than the maxillary deciduous central incisors, almost three-quarters of San individuals have incisors that are not as large as, or larger than, the canines.

The frequency distributions of relative canine size in the sexually pooled San and Negro samples are compared in Table 8 with these distributions for other populations as recorded by Hanihara (1955, 1966). It would appear that in Mongoloid peoples the percentage frequency of individuals with relatively large canines tends to be consistently lower than the corresponding frequencies

of Negro individuals. The Caucasoid sample studied by Hanihara (1966) has the highest frequency of individuals in whom the d^c is larger than the d^i . Comparison of the South African Negro frequency distributions with those of other populations (Table 9) indicated the differences to be not statistically significant, except in the case of Hanihara's (1955) Japanese sample. However, the frequency distributions of Hanihara's (1955, 1966) two Japanese samples are also significantly different. Thus, the percentage frequency of South African Negro individuals with relatively large canines is comparable to that in the other population groups sampled.

The San, however, shows a distributional pattern which is markedly different from that found in any other population, save Hanihara's (1955) Japanese sample, for which these frequencies have been recorded (Table 8). Comparison of the distribution frequencies encountered in the San sample with the frequencies recorded for other populations indicated the San distribution to be significantly different in each case except for Hanihara's (1955) Japanese sample (Table 9). The percentage of San individuals in whom the d^c

TABLE 9

Chi-square evaluation of distribution of individual index values above and below 100,0 per cent amongst the San, South African Negro, and other populations.
Sexually pooled samples.

<i>Comparative population</i>	x^2	<i>significance</i>
KALAHARI SAN COMPARISONS		
Japanese (Hanihara 1955) . . .	0,48	—
Japanese (Hanihara 1966) . . .	11,14	$p < 0,001$
Amerindian	18,55	$p < 0,001$
Eskimo	6,70	$p < 0,01$
Caucasoid	21,18	$p < 0,001$
American Negro	10,26	$p < 0,01$
Japanese-Caucasoid	12,19	$p < 0,001$
Japanese-Negro	4,58	$p < 0,05$
SOUTH AFRICAN NEGRO COMPARISONS		
Japanese (Hanihara 1955) . . .	13,08	$p < 0,001$
Japanese (Hanihara 1966) . . .	1,92	—
Amerindian	0,64	—
Eskimo	0,35	—
Caucasoid	1,00	—
American Negro	0,08	—
Japanese-Caucasoid	0,85	—
Japanese-Negro	1,78	—

is larger than the d^i is markedly smaller than this frequency recorded for any other population group, except the Japanese studied by Hanihara (1955). Apart from the fact that the Japanese sample examined by Hanihara in 1955

is about half as large as that studied by him in 1966, Hanihara has not provided an explanation for the significant differences in frequency distributions between these two samples.

DISCUSSION

Hanihara (1966, 1967, 1968, 1970) proposed that a relatively high canine-incisor index (i.e. values of about 105,0% and over) was distinctive of Caucasoid peoples and formed part of the 'Caucasoid dental complex'. Comparisons of canine-incisor indices for a larger series of population samples appear to support Hanihara's statements that Caucasoids tend to have higher mean index values than most other groups. Australoid peoples generally have lower mean indicial values, while Mongoloid populations tend to show intermediate values.

The canine-incisor index of the South African Negro is relatively high. In all three sets of comparisons (male, female, and sexually pooled samples) the mean Negro values fell within the observed Caucasoid ranges.

The canine-incisor index of the Kalahari San is, on average, rather low. In all three sets of comparisons the mean San values were found to be among the lowest computed for all populations.

Index values obtained for the American Negro tend to be high, falling within or even above observed Caucasoid mean ranges, and Hanihara (1967, 1970) has ascribed this to genetic admixture with American Caucasoids. Interestingly, while the canine-incisor index values of the South African Negro are also high, falling within the observed Caucasoid mean ranges but generally below the mean American Negro values, the index computed for the Liberian Negro is considerably lower than that shown by the South African Negro sample. Unfortunately, the data presented by Moss & Chase (1966) for Liberian Negroes and those given here for South African Negroes are the only measurements available at present for African Negro populations. More data will have to be accumulated for other African Negro samples before the rather marked difference in index values between the Liberian and South African Negroes can be explained adequately.

Perhaps the most striking features to emerge from this study are (i) the marked difference between the mean canine-incisor index values shown by the San and South African Negro populations, and (ii) the marked difference in the frequency distributions of individual index values among these samples.

The tendency towards a low mesiodistal canine-incisor index may be added to the list of osteological (De Villiers 1968; Grine 1979), somatic (Drury & Drennan 1926; Tobias 1955-1956, 1960, 1961, 1966; De Villiers 1961; Singer & Weiner 1963; Weiner *et al.* 1964), dental (Van Reenen 1961, 1964, 1966; Van Reenen & Dreyer 1963; Grine 1978, 1981), and genetic (Tobias 1972; Nurse & Jenkins 1977) features that characterize the San and serve to differentiate them from other African Negroid groups.

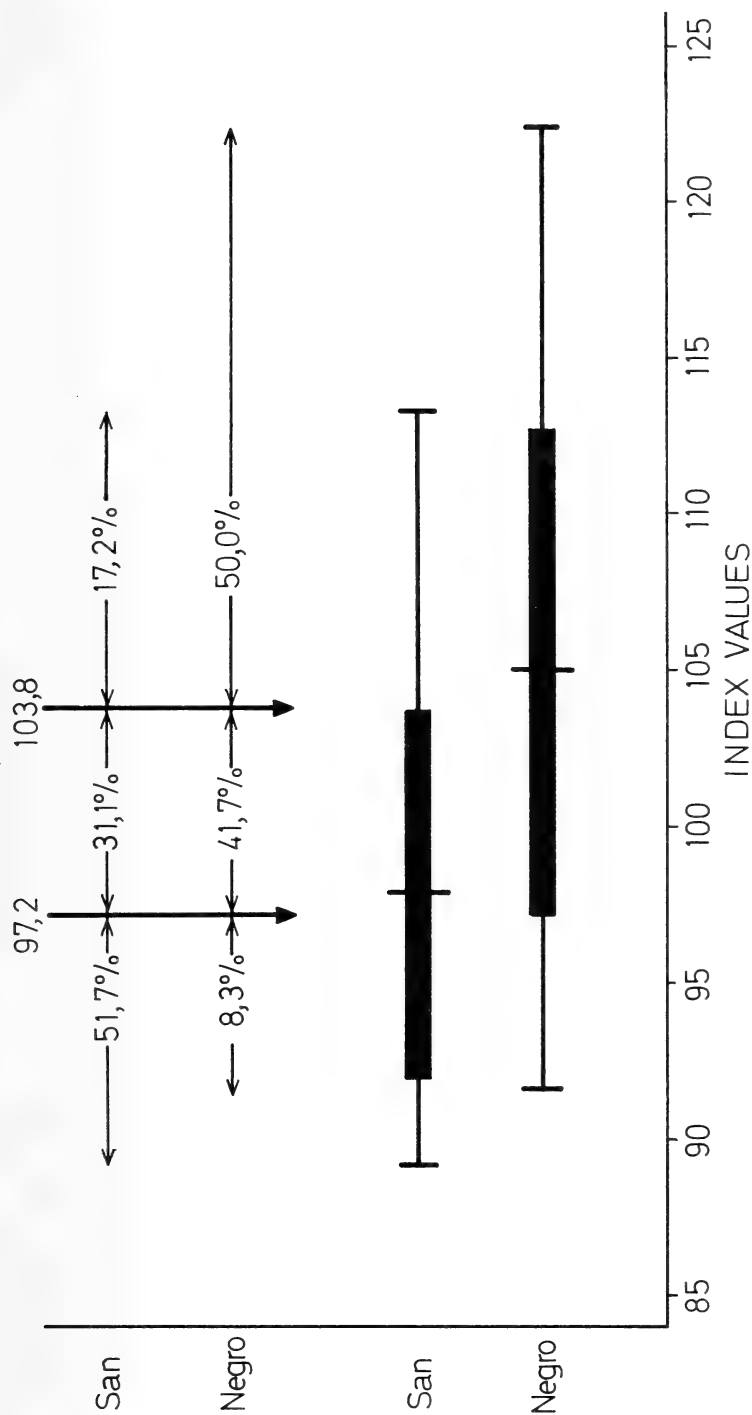


Fig. 1. Diagrammatic representation of the sexually pooled San and South African Negro sample ranges, means and means \pm one standard deviation of the mesiodistal canine-incisor index. Percentage figures represent frequencies of San and Negro individuals with index values above, below and between 97,2 (Negro $\bar{X} - 1$ SD) and 103,8 (San $\bar{X} + 1$ SD).

The mesiodistal canine-incisor index may serve as a useful tool to aid in the identification of human population samples from African, and especially southern African, archaeological sites. The racial identification of immature remains from such contexts is often difficult (Grine 1979) and it is in this regard that the canine-incisor index would appear to be of particular use. The discriminant reliability of this index, as with all other metrical and non-metrical characters of the dentition and skeleton, would be enhanced in circumstances where the population sample in question is of at least moderate size. Unfortunately, however, human remains from archaeological sites are often few in number.

In the identification of individual specimens, comparative sample ranges of a measurement are commonly used. There is a considerable degree of overlap in individual canine-incisor index values among the San and South African Negro (Figure 1, Table 1). Thus according to the data derived from the present samples of these two populations, a child with an index value of between 91,6 and 113,3 per cent could belong to either group. However, even if only one standard deviation on either side of the mean is used rather than the entire sample range, the utility of the mesiodistal canine-incisor index is noticeably increased.

For the present samples the upper extreme of one standard deviation of the San mean is a value of 103,75 per cent and the lower extreme of one standard deviation of the Negro mean is 97,21 (Fig. 1). Some 51,7 per cent of individuals comprising the San sample show index values below 97,21, while 50,0 per cent of Negro individuals examined have indicial values above 103,75.

SUMMARY

The relative mesiodistal diameters of the d^c and di^1 in samples of Kalahari San and South African Negro populations are investigated. The San tends to have a low canine-incisor index (i.e. the canines tend to be relatively small), while the Negro generally possesses a high canine-incisor index (i.e. the canines tend to be relatively large). Generally, Caucasoid samples have relatively high index values (Hanihara 1966, 1967, 1968, 1970), Australoid populations show relatively low values, and the indices of Mongoloid populations tend to be intermediate between these two extremes. The South African and American Negro index values but not the Liberian Negro index value are comparable to those displayed by Caucasoid samples. The mean San index is among the lowest computed for any human population.

The mean index values as well as the frequency distributions of individual index values are markedly different between the San and South African Negro. These differences are most apparent between the male and sexually pooled samples.

Used in conjunction with other dental and osteological features, the mesiodistal canine-incisor index may prove to be a useful tool in the identification

of human population samples from African, and especially southern African, archaeological sites. This index would appear to be particularly useful in the analysis of immature human remains.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

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Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

F. E. GRINE

RELATIVE SIZES OF THE
MAXILLARY DECIDUOUS CANINE AND
CENTRAL INCISOR TEETH
IN THE KALAHARI SAN (BUSHMAN)
AND SOUTH AFRICAN NEGRO

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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627-634.
KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309-320.
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THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269-270.

(continued inside back cover)

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THE OSTEOLOGY AND RELATIONSHIPS OF
TANGASAUROS MENNELLI HAUGHTON
(REPTILIA, EOSUCHIA)

By

PHILIP J. CURRIE

Cape Town Kaapstad

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THE OSTEOLOGY AND RELATIONSHIPS OF *TANGASAURUS MENNELLI* HAUGHTON (REPTILIA, EOSUCHIA)

By

PHILIP J. CURRIE

Provincial Museum of Alberta, Edmonton

(With 6 figures and 2 tables)

[MS accepted 11 November 1981]

ABSTRACT

The osteology of *Tangasaurus mennelli*, an eosuchian reptile from the Upper Permian of Tanzania, reveals a number of adaptations for an aquatic existence. Specimens from Madagascar that were attributed to *Tangasaurus mennelli* represent a distinct, as yet unnamed, genus that is related to *Tangasaurus* but less specialized. *Tangasaurus* is closely related to, but less specialized for an aquatic life than *Hovasaurus boulei* of the Upper Permian of Madagascar. The taxonomy of younginids and tangasaurids is re-examined, and it is concluded that these families together comprise a distinct taxonomic unit, the Younginoidea, that did not give rise to any other eosuchians.

CONTENTS

	PAGE
Introduction	247
Description	252
Skull	252
Vertebrae and ribs	253
Appendicular skeleton	256
Taxonomy	260
Superfamily Younginoidea superfam. nov.	260
Family Younginidae	260
Family Tangasauridae	262
Subfamily Kenyasaurinae subfam. nov.	262
Subfamily Tangasaurinae	262
Conclusions	263
Acknowledgements	264
References	264

INTRODUCTION

Eosuchians are generally considered to be the basal stock from which all later diapsids evolved. Recent papers by Carroll (1975, 1976a, 1976b, 1977, 1978), Currie (1980, 1981), Gow (1975), Harris & Carroll (1977), and Reisz (1977) have shown that eosuchians originated earlier and were more diverse than previously suspected. By the end of the Permian, at least three distinct lines had developed. One line is characterized by cervical elongation as in *Prolacerta* (Gow 1975) and the highly specialized *Tanystropheus* (Wild 1973). A separate lineage of eosuchians might have given rise to lizards (Carroll 1975) and the

gliding genus *Daedalosaurus* (Carroll 1978). *Youngina* is one of a diverse assemblage of terrestrial and aquatic forms that appears to have given rise to archosaurs (Carroll 1976a) and sauropterygians (Carroll 1981). The more detailed relationships of some of these taxa are considered here.

Four genera of reptiles seem to share a common ancestry with *Youngina*: *Tangasaurus* (Haughton 1924), a Late Permian reptile specialized for an aquatic existence, known from Tanzania; *Kenyasaurus* (Harris & Carroll 1977), a terrestrial relative of *Tangasaurus* from Lower Triassic strata of Kenya; and '*Datheosaurus*'* and *Hovasaurus* from Upper Permian beds of Madagascar. '*Datheosaurus*' was a terrestrial form like *Kenyasaurus*, whereas *Hovasaurus* was even more specialized for an aquatic existence than was *Tangasaurus*. Descriptions have recently been published on *Youngina* (Gow 1975) and *Kenyasaurus* (Harris & Carroll 1977), and papers on '*Datheosaurus*' and *Hovasaurus* are being prepared by Carroll and Currie respectively. The purpose of this paper is to redescribe the known specimens of *Tangasaurus* and to compare them with other tangasaurids.

In 1924 S. H. Haughton described two fossil reptile specimens that had been collected from Upper Permian strata in the vicinity of Tanga, in what is now Tanzania. These were recognized as a previously unknown taxon and named *Tangasaurus mennelli*. Although the specimens were designated as co-types, the smaller, better preserved one (Fig. 1A) is here considered as the lectotype. It is in the museum in Bulawayo, Zimbabwe, while its counterpart, SAM-6231 (Fig. 1B), and the larger specimen, SAM-6232 (Fig. 1C), are in the South African Museum, Cape Town. On the basis of postcranial characteristics, Haughton (1924) felt that *Tangasaurus* was probably a diapsid reptile that, because of the long, powerful, flattened tail, had become adapted for an aquatic existence.

Numerous specimens of small reptiles had been collected in beds of approximately the same age along the Sakamena River of southern Madagascar. One of the animals collected was described as *Broomia madagascariensis* (Piveteau 1925), but was referred the following year by Piveteau to *Tangasaurus menelli* (*sic*). Contrary to Haughton, Piveteau felt that *Tangasaurus* was a primarily terrestrial animal. Following Nopcsa (1924), he considered it to be related to *Araeoscelis*, *Kadaliosaurus*, *Broomia*, *Saurosternon*, and *Pleurosaurus*.

A new genus and species, *Hovasaurus boulei*, also from Madagascar, described by Piveteau (1926) was considered to be related to *Mesosaurus*. Although not as specialized as *Mesosaurus* for living in the water, Piveteau felt that the short neck, short manus, well developed haemal spines and slight pachyostosis of the ribs showed that *Hovasaurus* was an aquatic animal.

Haughton (1930) restudied Piveteau's specimens from Madagascar, concluding that *Tangasaurus* and *Hovasaurus* were allied and that both were diapsids. *Hovasaurus* was recognized as a reptile adapted to an aquatic existence through reduction of the forelimb and coracoid, and retarded ossification and

* While this paper was in press '*Datheosaurus*' specimens were redescribed as *Thadeosaurus* (Carroll 1981).

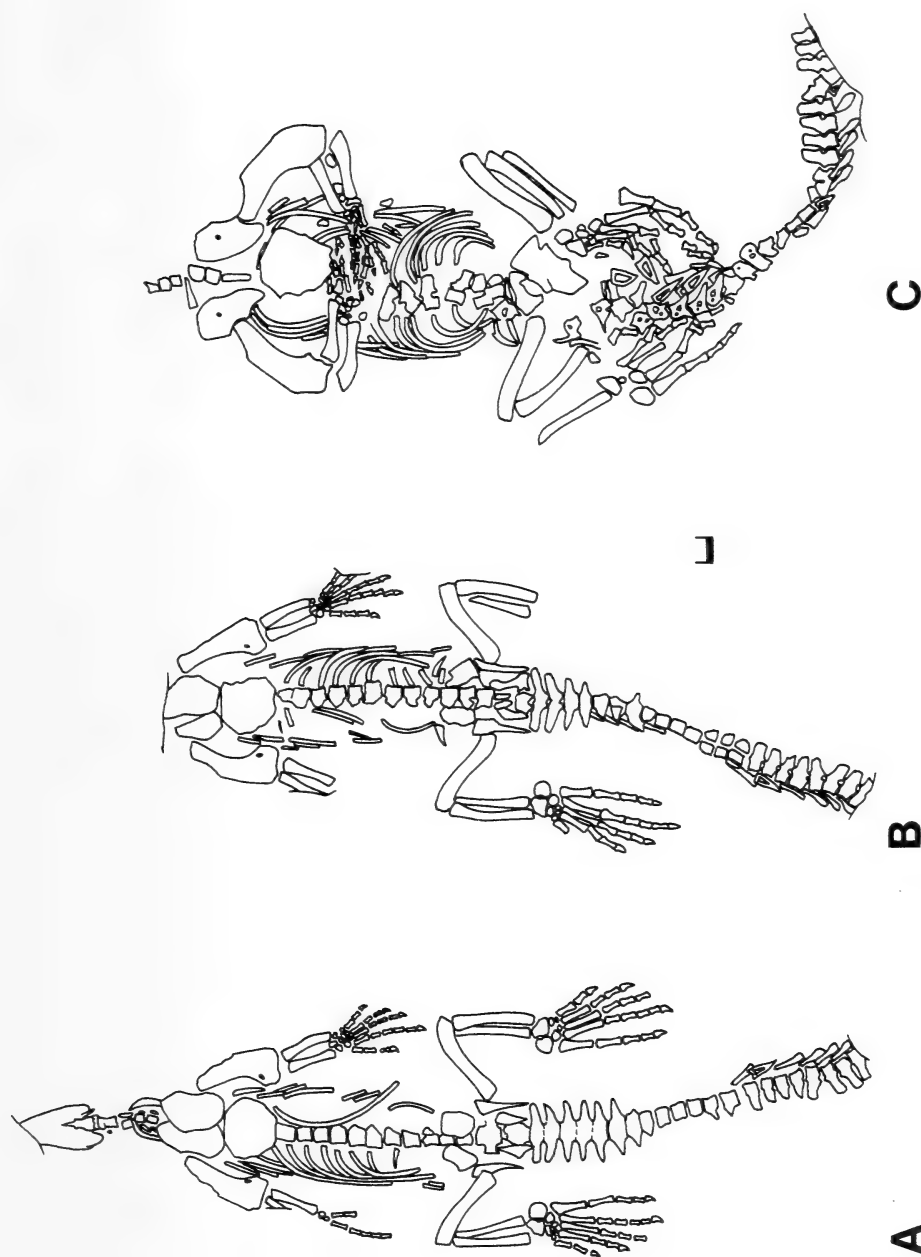


Fig. 1. *Tangasaurus menelli*. A. Ventral view of lectotype in Bulawayo Museum, Zimbabwe. B. SAM-6231, counterpart of preceding specimen (from Harris & Carroll 1977). C. SAM-6232, ventral view. Scale = 1 cm.

elongation of the body. *Tangasaurus* was considered to be morphologically intermediate between *Youngina* and *Hovasaurus*.

Other specimens described by Piveteau (1926) were not associated with *Tangasaurus* and *Hovasaurus* until recently. A large number of caudal sections were recovered along the Sakamena River of Madagascar. The caudal vertebrae have high neural spines, and the haemal spines are long and plate-like. Piveteau recognized these as belonging to a reptile adapted to swimming, but did not have any other skeletal elements associated with the caudal vertebrae. These are now known to belong to *Hovasaurus*.

A third genus recognized by Piveteau (1926: 171–172) was assigned with doubt to the European genus *Datheosaurus*, now considered to be congeneric with *Haptodus* (Currie 1979), a sphenacodont pelycosaur. The specimens referred to this genus were restudied recently by Carroll (1981) who considers them to be a new genus. Morphologically this animal appears to be close to the ancestral stock of *Tangasaurus* and *Hovasaurus*.

Kenyasaurus mariakeniensis from the Lower Triassic of Kenya (Harris & Carroll 1977) is considered to be most closely comparable with *Tangasaurus* and *Hovasaurus* on the basis of general body form, the presence of a sternum and, particularly, the anatomy of the foot.

Piveteau (1926) included *Broomia*, *Saurosternon* and *Tangasaurus* in the Tangosaurinae (*sic*). After Haughton's paper of 1930 demonstrated the anatomical similarities between *Tangasaurus* and *Hovasaurus*, these genera were usually included as the only representatives of the family Tangosauridae (Camp 1945; Romer 1956, 1966; Piveteau 1955; Orlov 1964; Kuhn 1969). Depending on how the various authors have classified primitive diapsid reptiles, the Tangosauridae have been referred to the Araeosceloidea (Nopcsa 1924; Piveteau 1926), Eosuchia (Haughton 1930; Von Huene 1940, 1952; Piveteau 1955; Romer 1956, 1966; Kuhn 1969), Prolacertilia (Watson 1957; Orlov 1964) or Protorosauria (Camp 1945).

In re-examining the anatomy of tangasaurids, it became obvious that there is a great deal of confusion concerning the identification and anatomy of these animals. The anatomy of *Tangasaurus* and *Hovasaurus* is very similar, and there are few characters to distinguish these genera. Although more than 300 tangasaurid specimens were collected in Madagascar, in almost every case two of the most diagnostic parts of the body—the skull and the tail—were missing. The problem is compounded by poor preservation of the type specimens of *Tangasaurus mennelli* from Tanzania that generally have been ignored in favour of the better preserved specimens from Madagascar. Finally, many of the specimens have been misidentified because they are immature and show few distinctive characters. As part of a revision of tangasaurid anatomy, the majority of specimens that have been figured were re-examined and, in many cases, re-identified (Table 1). Hopefully, the confusion concerning the identification of tangasaurids has been resolved. This will permit more accurate conclusions concerning evolutionary and developmental lineages, palaeoecology, geographic

TABLE 1
Figured specimens of Tangosauridae.

Identification (this paper)	Specimen number	Previous identification
' <i>Datheosaurus</i> '	MNHN 1908-5-1	<i>Tangasaurus mennelli</i> (Piveteau 1926, pl. 12 (fig. 1))
' <i>Datheosaurus</i> '	MNHN 1908-11-4	<i>T. mennelli</i> (Piveteau 1926, pl. 10 (fig. 2))
' <i>Datheosaurus</i> '	MNHN 1908-11-5	<i>T. mennelli</i> (Piveteau 1926, pl. 11 (fig. 2), text-figs 17-18; Piveteau 1955, fig. 9; Gladstone & Wakeley 1932 fig. 2; Kuhn 1969, figs 18-6, 18-8)
' <i>Datheosaurus</i> '	MNHN 1908-11-6	<i>T. mennelli</i> (Piveteau 1926, pl. 16 (fig. 2))
' <i>Datheosaurus</i> '	MNHN 1908-11-7	<i>T. mennelli</i> (Piveteau 1926, pl. 10 (fig. 1))
' <i>Datheosaurus</i> '	MNHN 1908-11-19	? <i>Datheosaurus</i> sp. (Piveteau 1926, pl. 17 (fig. 2))
<i>Hovasaurus boulei</i>	MNHN 1908-21-2	<i>Hovasaurus boulei</i> (Piveteau 1926, pl. 8 (fig. 2))
<i>H. boulei</i>	MNHN 1908-21-7	<i>H. boulei</i> (Piveteau 1926, pl. 8 (fig. 1); Haughton 1930, fig. 3C)
<i>H. boulei</i>	MNHN 1908-21-8	<i>H. boulei</i> (Piveteau 1926, pl. 7 (fig. 1))
<i>H. boulei</i>	MNHN 1908-21-10	<i>T. mennelli</i> (Harris & Carroll 1977, text-fig. 5B)
<i>H. boulei</i>	MNHN 1908-21-11	Indeterminate reptile (Piveteau 1926, pl. 10 (fig. 4))
<i>H. boulei</i>	MNHN 1908-21-16	<i>T. mennelli</i> (Piveteau 1926, pl. 15 (fig. 5) text-fig. 20; Gladstone & Wakeley 1932, text-fig. 2)
<i>H. boulei</i>	MNHN 1908-32-22	<i>H. boulei</i> (Piveteau 1926, pl. 9 (fig. 4), text-fig. 14)
<i>H. boulei</i>	MNHN 1908-32-23	<i>H. boulei</i> (Piveteau 1926, pl. 9 (figs 1-2, text-fig. 16)
<i>H. boulei</i>	MNHN 1908-32-24	<i>T. mennelli</i> (Piveteau 1926, pl. 13 (fig. 1); Harris & Carroll 1977, text-fig. 5A)
<i>H. boulei</i>	MNHN 1908-32-25	<i>T. mennelli</i> (Piveteau 1926, pl. 14 (fig. 3))
<i>H. boulei</i>	MNHN 1908-32-26	<i>T. mennelli</i> (Piveteau 1926, pl. 15 (fig. 1))
<i>H. boulei</i>	MNHN 1908-32-29	<i>H. boulei</i> (Piveteau 1926, pl. 7 (fig. 2))
<i>H. boulei</i>	MNHN 1925-5-30	<i>H. boulei</i> (Piveteau 1926, pl. 9 (fig. 3), text-fig. 12)
<i>H. boulei</i>	MNHN 1925-5-31	<i>T. mennelli</i> (Piveteau 1926, pl. 15 (fig. 4), text-fig. 22; Piveteau 1955, text-fig. 10)
<i>H. boulei</i>	MNHN 1925-5-32	<i>T. mennelli</i> (Piveteau 1926, pl. 16 (fig. 1), text-fig. 23; Haughton 1930, text-fig. 4C; Piveteau 1955, text-fig. 11; Kuhn 1969, text-fig. 18-7; Harris & Carroll 1977, text-fig. 5C)
<i>H. boulei</i>	MNHN 1925-5-33	<i>T. mennelli</i> (Piveteau 1926, pl. 10 (fig. 3))
<i>H. boulei</i>	MNHN 1925-5-34	<i>T. mennelli</i> (Piveteau 1926, pl. 14 (fig. 2); Camp 1945, text-fig. 10)
<i>H. boulei</i>	MNHN, number unknown	<i>H. boulei</i> (Piveteau 1926, pl. 7 (fig. 3); Haughton 1930, text-fig. 1A)
? <i>H. boulei</i>	MNHN, number unknown	<i>T. mennelli</i> (Piveteau 1926, pl. 13 (fig. 5), pl. 14, fig. 1)
<i>Kenyasaurus mariakaniensis</i>	KNM-MA1	<i>Kenyasaurus mariakaniensis</i> (Harris & Carroll 1977, text-figs 1-4)
<i>Tangasaurus mennelli</i>	SAM-6231	<i>Tangasaurus mennelli</i> (Haughton 1924, pl. 2, text-figs 1-3; Von Huene 1926, text-fig. 33; Romer 1956, text-fig. 186E; Orlov 1964, text-fig. 468; Kuhn 1969, text-figs 17-12; Harris & Carroll 1977, text-fig. 6)
<i>T. mennelli</i>	SAM-6232	<i>T. mennelli</i> (Haughton 1924, pl. 1)
Not a tangasaurid	MNHN 1909-3-30	<i>T. mennelli</i> (Piveteau 1926, pl. 15 (figs 2-3))
Not a tangasaurid	MNHN, number unknown	<i>T. mennelli</i> (Piveteau 1926, pl. 13 (figs 2, 2A))
Not a tangasaurid	MNHN, number unknown	<i>T. mennelli</i> (Piveteau 1926, pl. 13 (fig. 3))
Not a tangasaurid	MNHN, number unknown	<i>T. mennelli</i> (Piveteau 1926, pl. 13 (figs 4, 4A))

distribution and stratigraphy. One unfortunate result is that *Tangasaurus* can no longer be used for biostratigraphic correlation of the middle division of the Tanga beds of Tanzania with the Lower Sakamena Formation of Madagascar (McKinlay 1956, 1960).

Tangasaurid eosuchians were relatively small lizard-like reptiles. The largest is *Hovasaurus* with an estimated maximum snout-vent length of about 30 cm. The largest specimen of *Tangasaurus* is 20 per cent smaller than the largest *Hovasaurus*, but it can be inferred from the incompleteness of ossification that larger specimens probably existed. The linear dimension of a mature specimen of '*Datheosaurus*' are about 35 per cent smaller than the same dimensions in *Hovasaurus*. Proportions and lengths listed in this paper for *Hovasaurus* and '*Datheosaurus*' were estimated for adult size from the allometric growth curves.

Hovasaurus and *Kenyasaurus* are valid genera. Use of the name *Tangasaurus* in this paper is restricted to the two specimens from Tanzania. When referring to generic characters attributed by Piveteau (1926), Houghton (1930), and others to specimens from both Tanzania and Madagascar, the name *Tangasaurus* will be used in quotation. '*Datheosaurus*' is used to refer to most of the specimens from Madagascar that Piveteau (1926) identified as *Datheosaurus* and *Tangasaurus*.

The following abbreviations have been used when giving specimen numbers:

MNHN, Muséum National d'Histoire Naturelle
SAM, South African Museum

DESCRIPTION

SKULL

Cranial anatomy is poorly known in tangasaurids. In one of the two known specimens of *Tangasaurus*, the poorly preserved skull is exposed in palatal aspect. The bone is crushed flat, and seems little better than a film of carbon. Further preparation of the specimen seems unfeasible. The anterior portion of the skull was not collected, but the preserved portion is 38 mm in length. Houghton (1924) felt that the full length of the skull would have been between 50 and 60 mm. In the light of the anterior tapering of the skull, there was probably no elongate snout, and it is doubtful that the skull would have exceeded 45 mm. The only bone that can be identified with any degree of certainty is the basisphenoid-parasphenoid complex. The cultriform process is long and tapering, and the basiptyergoid processes appear to be short. The complex is concave ventrally in transverse section between the tuberosities. Houghton (1924) made observations on the pterygoid and various palatal vacuities, but none of these can be seen clearly enough in the specimen to merit description. The basioccipital can be seen at the back of the skull, but shows no distinctive characters. Von Huene (1926) identified one bone as either stapes or

quadrate, but whatever it is, the bone gives us no better understanding of the skull.

Only the postorbital and palatal regions of the skull of *Hovasaurus* are known. The contours and proportions of the parasphenoid-basisphenoid complex of *Tangasaurus* are similar to those of *Hovasaurus*.

VERTEBRAE AND RIBS

Haughton (1924) estimated that there were eighteen presacral vertebrae in the lectotype (SAM-6231) of *Tangasaurus mennelli*. This number is much less than that of other eosuchians, and it is assumed that he had not included the cervical vertebrae in his total. Because he stated that there were seven or fewer anterior vertebrae obscured by bones of the pectoral girdle, his estimated presacral count can be raised to a maximum of twenty-five. This is the number of vertebrae found in *Hovasaurus*. As in *Hovasaurus*, the neck of *Tangasaurus* is short—probably including only five vertebrae.

Primitive diapsid reptiles characteristically have two sacral vertebrae. Haughton (1924: 3) stated that one specimen of *Tangasaurus mennelli* (SAM-6231) had three fused sacral vertebrae. However, preservation in the sacral region of this specimen is poor, and it is likely that he misinterpreted the first caudal rib as a sacral rib. In a later paper Haughton (1930) stated that '*Tangasaurus*' has two sacrals.

The total length of the tail is known in few eosuchians. 24 caudal vertebrae are preserved in the lectotype of *Tangasaurus*, and 28 in SAM-6232. However, the tail was clearly much longer than this. '*Datheosaurus*' has at least 45 caudals and *Hovasaurus* probably had more than 70.

Details of the dorsal vertebrae are difficult to delineate in the type specimens of *Tangasaurus*. In *Hovasaurus*, there is a process at the base of the neural spine that acts as an extra intervertebral articulation (Fig. 2). A similar accessory process appears to be present in at least one of the dorsal vertebrae of the larger specimen of *Tangasaurus*. Contact between the neural spines has also been noted in *Youngina* (Currie 1981), '*Datheosaurus*', and *Kenyasaurus*.

Specimens of *Tangasaurus* (Figs 3A–B, 4) have caudal vertebrae that are specialized for propulsion in water. The neural spines are high and the haemal spines are long and expanded distally. The neural spines of the mid-caudals are higher than the presacral neural spines, but are not as long as the haemal spines. The specialization is not as great as in *Hovasaurus* (Fig. 3D) in that the neural spines are relatively lower, only about 35 per cent greater than the length of the associated centrum compared with more than 125 per cent in *Hovasaurus*. Nevertheless, the caudal specialization suggests that *Tangasaurus* and *Hovasaurus* are closely related. Specimens from Madagascar attributed to '*Tangasaurus*' and '*Datheosaurus*' have unspecialized caudal vertebrae with low neural spines (Fig. 3C).

The dorsal ribs of *Tangasaurus* have a single head and are not pachyostotic.

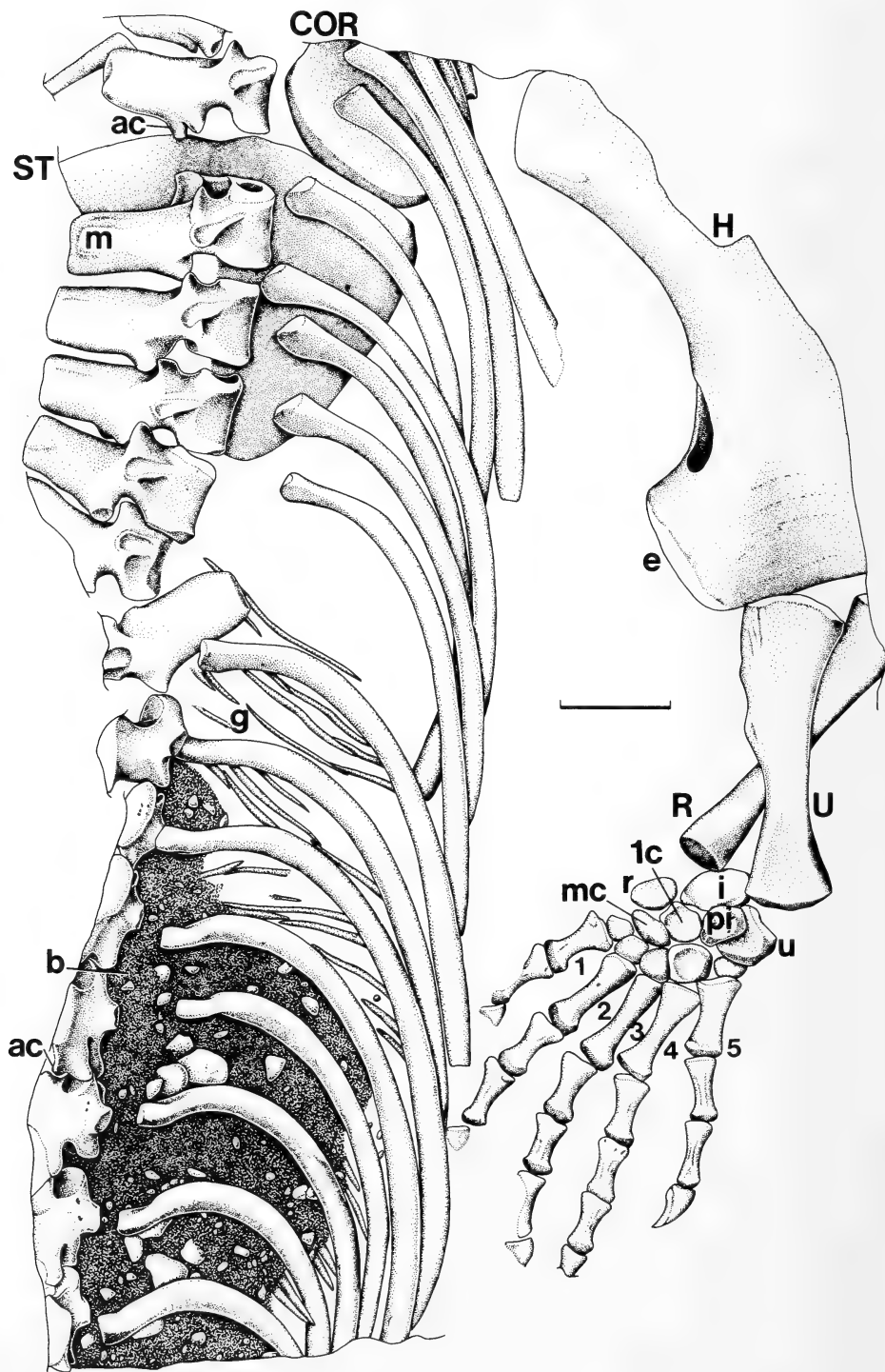


Fig. 2. *Hovasaurus boulei*, MNHN 1908-32-59. Abbreviations: ac—accessory articulation on neural spine, b—ballast, COR—coracoid, e—entepicondyle, g—gastralia, H—humerus, i—intermedium, lc—lateral centrale, m—mammillary process, mc—medical centrale, pi—pisiform, R—radius, r—radiale, ST—sternum, U—ulna, u—ulnare. Scale = 1 cm.

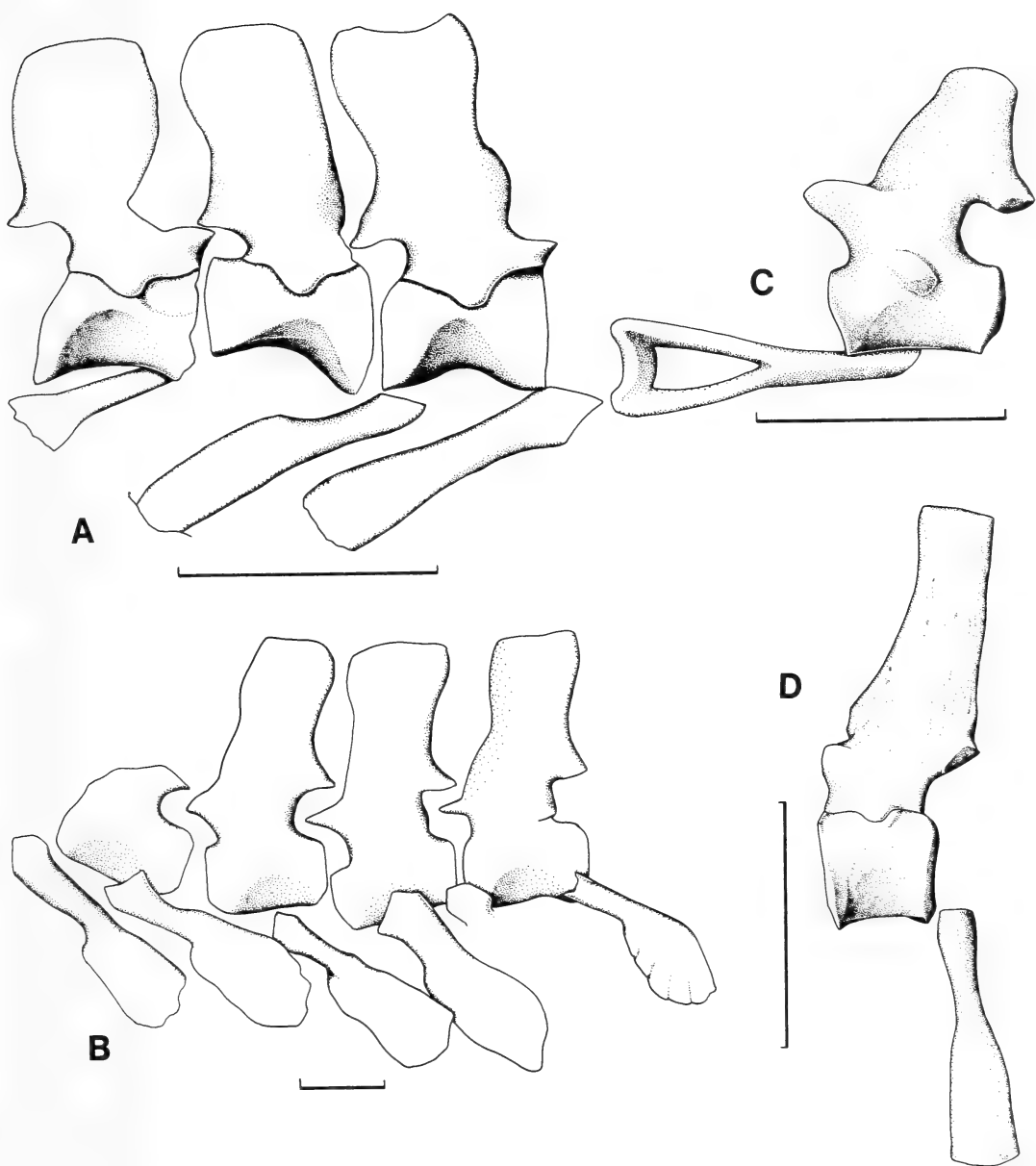


Fig. 3. Caudal vertebrae of tangasaurid eosuchians. A. *Tangasaurus* (Bulawayo Museum), 19th to 21st, right aspect. B. *Tangasaurus*, SAM-6232, 20th to 23rd, left view. C. '*Datheosaurus*', MNHN 1908-5-1, mid-caudal, left view. D. *Hovasaurus*, MNHN 1908-32-64, 14th caudal, left aspect. Each scale = 1 cm.

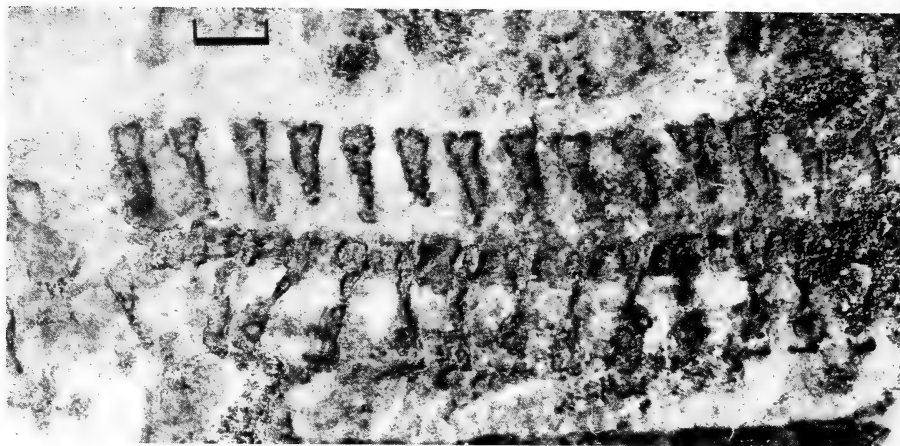


Fig. 4. *Tangasaurus mennelli*, SAM-6233, caudal vertebrae. Scale = 1 cm.

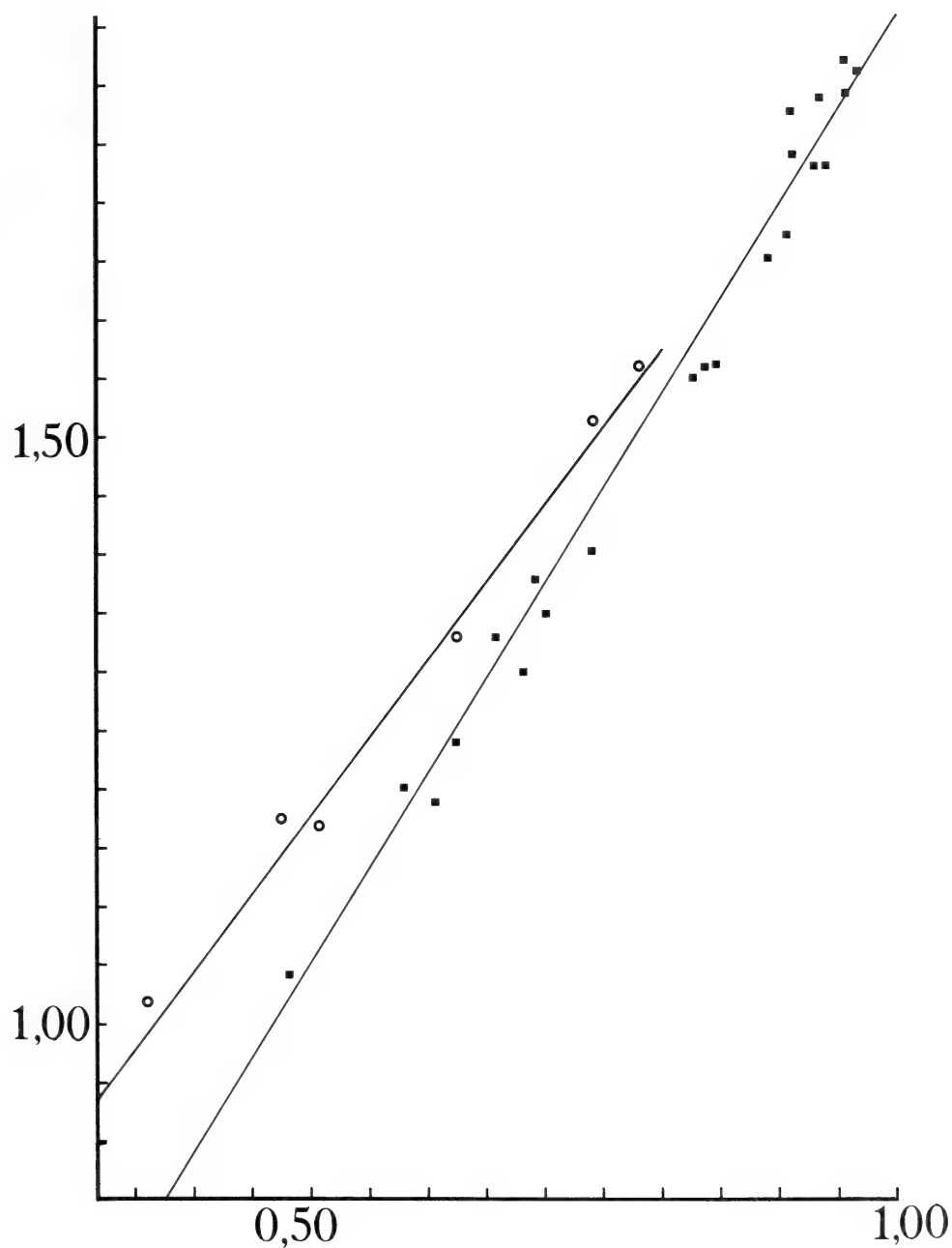
In *Hovasaurus*, moderate pachyostosis can be seen in the ribs of large individuals but it is usually not apparent in juveniles.

An exact count of caudal ribs is not possible because of the poor preservation of the *Tangasaurus* specimens. The total number, however, would have been between 9 and 12. There are a maximum of 12 pairs of caudal ribs in *Hovasaurus* and an additional 2 pairs of transverse processes. Nineteen pairs of caudal ribs and transverse processes are found in specimens from Madagascar that were formerly attributed to *Tangasaurus*, and 28 pairs in *Kenyasaurus*.

APPENDICULAR SKELETON

Both Piveteau (1926) and Haughton (1924, 1930) recognized that the relative lengths of elements of the appendicular skeleton change with age. More precise calculations (Currie in preparation) have shown that '*Tangasaurus*' specimens of Madagascar are juveniles of '*Datheosaurus*', and that the allometric growth coefficients for '*Datheosaurus*' and *Hovasaurus* are different (Fig. 5).

The two specimens of *Tangasaurus* represent animals of different ages and consequently show some differences in limb proportions. Comparison can be made with *Hovasaurus* by means of the allometric growth equations. The constants b' and k_{yx} power equation $y = b'x^{k_{yx}}$ (Currie 1978) were solved to describe a growth series of *Hovasaurus boulei*. The average length of a dorsal centrum that serves as the base for comparison is represented by x , while the length of the element being compared is represented by y . From this information, the expected mean length (in millimetres) of each element was computed for *Hovasaurus* specimens of the same size as the *Tangasaurus* specimens SAM-6231 ($x = 6,6$ mm) and SAM-6232 ($x = 8,0$ mm). Lengths of the metacarpals and metatarsals were not included in the lengths of the digits of the manus and



pes. With the exception of the length of metatarsal IV of SAM-6231 and the length of digit IV of the pes of SAM-6232, all measurements fell within the 95 per cent confidence intervals for these dimensions in *Hovasaurus* (Table 2). This shows that the relative lengths of limb elements are almost the same in *Tangasaurus* and *Hovasaurus*, which also suggests close relationship because of the specialized proportions of *Hovasaurus* limbs for swimming.

In the smaller specimen of *Tangasaurus* (SAM-6231), the humerus is shorter than the femur, whereas the femur is the shorter of the two in the larger specimen. This suggests that the humerus grew faster than the femur as the animal increased in size. The same thing happens in both '*Datheosaurus*' and *Hovasaurus* where more complete growth series are known. Haughton (1930) stated that the limbs of '*Tangasaurus*' are longer relative to the body than those of *Hovasaurus*. However, it is now known that the humerus of *Tangasaurus* is 5.8 times the length of a dorsal centrum (\bar{x}), that of a mature '*Datheosaurus*' is 6.7x, and that of a mature specimen of *Hovasaurus* is 7.1x. Similarly, other limb elements of *Tangasaurus* have slightly smaller relative lengths than the same elements in *Hovasaurus*.

In *Tangasaurus*, the radius is 60 per cent the length of the humerus,

TABLE 2

Comparisons of the lengths of postcranial elements of *Hovasaurus boulei* and *Tangasaurus mennelli*. The constants b' and k_{yx}' of the power equation $y = b'x^{k_{yx}'}$ have been solved to describe growth series of *H. boulei*. From this information, the expected mean lengths (in mm) of each element have been computed for *H. boulei* specimens the same size as the co-types of *T. mennelli* ($x = 6.6$ mm for SAM-6231, 8.0 mm for SAM-6232). Lengths of the metacarpals and metatarsals are not included in the lengths of the digits of the manus and pes. Abbreviations: N—size of sample, R—correlation coefficient.

y = length of	N	R	k_{yx}'	b'	x	Estimated mean value of y for <i>H. boulei</i> 95% confidence interval	Measured value of y for <i>T. mennelli</i>
Coracoid	9	0.981	2.229	0.360	6.6 8.0	24.1 37.0	25.3 31.7
Sternum	15	0.987	1.780	0.739	6.6 8.0	22.1 29.9	21.8 30.3
Humerus	20	0.993	1.638	1.674	6.6 8.0	36.8 50.5	36.0 48.5
Radius	13	0.994	1.306	1.893	6.6 8.0	22.2 28.6	21.6 28.0
Metacarpal IV	12	0.991	1.354	0.599	6.6	7.7	8.0
Digit IV (manus) .	12	0.983	1.236	2.035	6.6	20.9	21.0
Ilium	14	0.996	1.067	2.952	6.6	22.1	23.0
Femur	16	0.990	1.334	3.146	6.6 8.0	39.0 50.4	39.0 47.2
Tibia	15	0.991	1.298	2.872	6.6 8.0	33.2 42.6	34.0 40.0
Metatarsal IV	14	0.995	1.340	1.310	6.6 8.0	16.4 21.2	17.4 20.5
Digit IV (Pes)	9	0.991	1.493	1.996	6.6 8.0	33.3 44.5	32.2 39.1

whereas in mature *Hovasaurus* it is only 52 per cent. In the relatively unspecialized '*Datheosaurus*' the radius is 54 per cent the length of the humerus at maturity. Relative to the length of a dorsal centrum, however, the length of the forearm of *Tangasaurus* is only 3,3 \bar{x} , whereas that of *Hovasaurus* is the same as '*Datheosaurus*' (3,7 \bar{x}). This contradicts Haughton's (1930) statement that the forearm is relatively shorter in *Hovasaurus*. It should be remembered that his statement is true for immature specimens, and he did not have a complete growth series available to him.

The tibia is 85 per cent the length of the femur in *Tangasaurus* and *Hovasaurus* at maturity, and 90 per cent in '*Datheosaurus*'.

Many eosuchians, including *Youngina* (Broom 1922), *Tangasaurus* (Fig. 1), *Hovasaurus* (Piveteau 1926), '*Datheosaurus*' (Piveteau 1926) and *Kenyasaurus* (Harris & Carroll 1977), have ossified sterna. The dimensions and outline of the sternum of *Tangasaurus* fall within the range of *Hovasaurus*.

The coracoids of *Tangasaurus* and *Hovasaurus* are similar in outline. Haughton (1930) stated that they are distinguishable on the basis of proportions, but the coracoids of the type specimen of *Tangasaurus mennelli* are too poorly preserved to confirm this statement.

The humeri of *Tangasaurus* are identical in outline to those of many specimens of *Hovasaurus*. Well-ossified humeri of *Tangasaurus*, *Hovasaurus*, and '*Datheosaurus*' share the distinctive feature of a greatly expanded entepicondyle (Figs. 1–2). The width of the distal end of the humerus is up to 40 per cent of its length. It is worth noting that the known humeri of *Youngina* are all from immature animals and consequently do not show a well-ossified entepicondyle. However, the curvature at the base of the entepicondyle and the position of the entepicondylar foramen suggest that the humerus of mature individuals of *Youngina* also had a greatly expanded entepicondyle.

The tarsus of *Tangasaurus*, *Hovasaurus*, *Kenyasaurus*, and '*Datheosaurus*' is specialized in the loss of the fifth distal tarsal as a discrete element. Harris & Carroll (1977) refer to a specimen of *Hovasaurus* (MNHN 1908–21–10) and suggest that the fifth and fourth distal tarsals fuse at maturity.

A very distinctive characteristic of most specimens of *Hovasaurus* is the presence of abundant pebbles, mainly quartz, in the abdominal cavity (Fig. 2). It was assumed (Haughton 1930) that these were gastroliths, but they seem to be too numerous, large, and closely packed to have functioned effectively in food breakdown. Considering the apparent aquatic habits of *Hovasaurus*, it may be more appropriate to consider them as having served as ballast. The same function appears to be true for 'gastroliths' of crocodiles (Cott 1961) and plesiosaurs (Darby & Ojackangas 1980). Stomach stones are found in at least one specimen of '*Datheosaurus*' (MNHN 1908–11–5), (Piveteau 1926, pl. 11) but are few in number and possibly did serve as aids to digestion. When present, the relative abundance of stomach stones is a quick way to distinguish *Hovasaurus* from '*Datheosaurus*'. Absence of stomach stones from the *Tangasaurus* specimens does not necessarily mean that this genus did not swallow pebbles. Some

specimens of *Hovasaurus* do not have stones in the abdomen, so this may possibly be explained as post-mortem rupture of the abdominal cavity before the cadaver came to rest and was buried by sediment.

TAXONOMY

In the light of improved knowledge of the morphology of the tangasaurids, it is possible to establish a diagnosis for the family. The relationship of the Tangasauridae to *Youngina* will be considered here as well.

In recent years, it has become widely accepted that a proper taxonomic diagnosis should emphasize derived (advanced) character states rather than the retention of primitive characters. Characters listed in the following suprageneric diagnoses are derived and can be used to distinguish the taxa from all known eosuchian taxa that are not considered in this paper. Numbers in parentheses refer to Figure 6.

Class REPTILIA Linnaeus, 1758

Subclass LEPIDOSAURIA Duméril & Bibron, 1839

Order EOSUCHIA Broom, 1914

Suborder YOUNGINIFORMES Romer, 1945

Superfamily YOUNGINOIDEA superfam. nov.

Fig. 6

Diagnosis

Distinctive sutures on parietal for frontal and postfrontal (1). Accessory intervertebral articulation present on mid-line of dorsal neural spine (2). Ossification of paired sternal plates into a single unit in mature animals (3). Entepicondyle of humerus strongly developed at maturity (4). Olecranon process and sigmoidal notch of ulna poorly developed in mature animals (5); radius longer than shaft of ulna (6).

Family **Younginidae** Broom, 1914

Youngina Broom, 1914

Diagnosis

3 premaxillary, 15–23 maxillary, and 20 dentary teeth. Zygapophyses of anterior dorsal vertebrae extend laterally beyond the centra and inclined at low angle from horizontal; neural spines low and rectangular. Iliac blade short and almost vertical. Humerus only about 70 % length of femur, compared with 75 % in immature *Hovasaurus* and 110 % in mature *Hovasaurus*. Radius 80 % length of humerus, and 60 % length of tibia; tibia 90 % length of femur. Proximal head of fifth metatarsal expanded but not hooked.

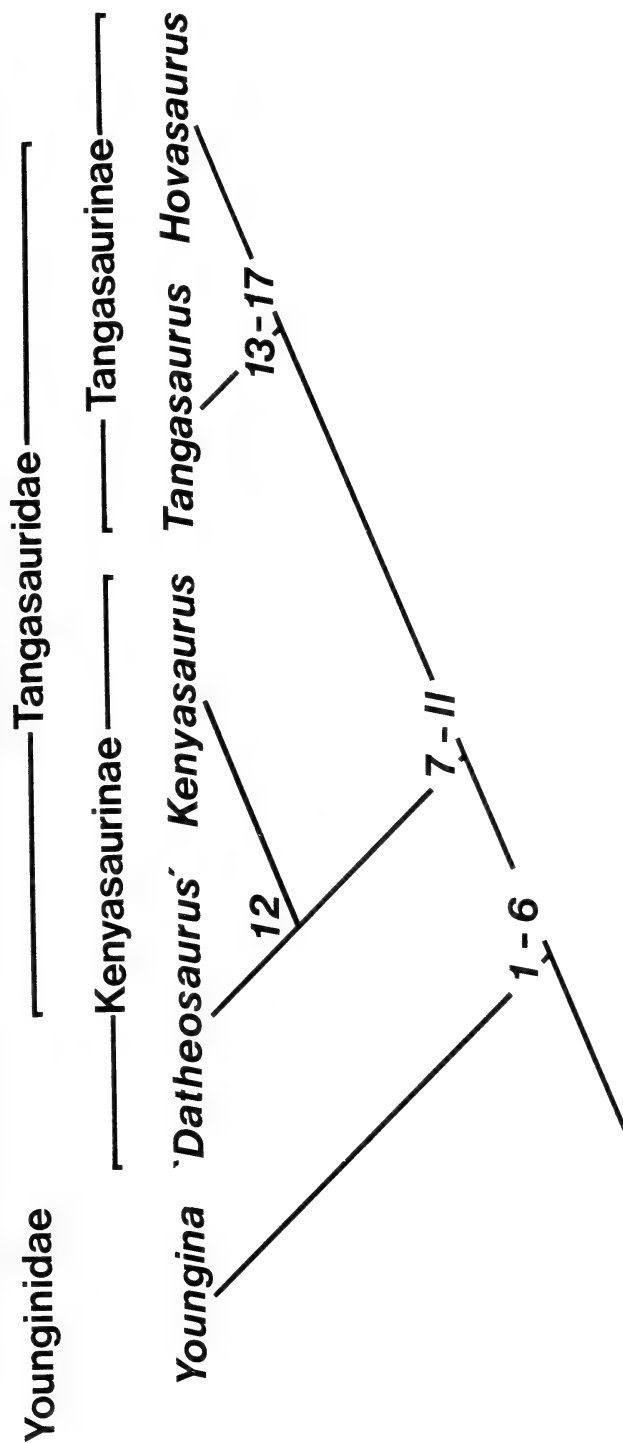


Fig. 6. Phylogenetic chart showing the apparent interrelationships of younginoid eosuchians. Numbers refer to characters discussed in the text.

Family **Tangasauridae** Camp, 1945*Diagnosis*

Humerus as long as or longer than femur in mature animals (7); radius 50–65 per cent length of humerus and 65–75 per cent length of tibia at maturity. Scapula low in lateral aspect and mainly a ventral element (8); coracoid as large as the scapula (9). Medial centrale contacts fourth distal carpal, thereby preventing contact between the lateral centrale and third distal carpal (10). Fifth distal tarsal not a discrete element (11).

Subfamily **Kenyasaurinae** subfam. nov.*Diagnosis*

19–28 pairs of caudal ribs and transverse processes present, all of which taper distally (12).

Kenyasaurus Harris & Carroll, 1977*Type species*

Kenyasaurus mariakaniensis Harris & Carroll 1977: 140.

Diagnosis

Low but anteroposteriorly elongate neural spines in the dorsal region; 56 caudal vertebrae; 28 pairs of caudal ribs and transverse processes. Astragalus almost triangular rather than primitive L-shape; pronounced process on fifth metatarsal for insertion of peroneus brevis.

Thadeosaurus colcanapi Carroll, 1981

Broomia madagascariensis Piveteau, 1925: 157.

Datheosaurus sp., Piveteau, 1926: pl. 17 (fig. 2).

Tangasaurus menelli, Piveteau, 1926: pl. 10 (figs 1–2), pl. 11 (figs 1–2), pl. 12 (fig. 1), pl. 16 (fig. 2).

Diagnosis

Neural spines tall and rectangular in dorsal region; 47 caudal vertebrae; 19 pairs of caudal ribs and transverse processes. Small numbers of gastroliths present in abdominal cavities of some specimens.

Subfamily **Tangasaurinae** Piveteau, 1926*Diagnosis*

Neural spines high in dorsal region and higher in proximal and mid-caudal regions (13). 9–12 pairs of caudal ribs (14); anterior caudal ribs expanded distally (15); haemal spines large and platelike (16). Presacral intercentra, with the exception of the first three, do not ossify until animal is mature (17).

Tangasaurus Haughton, 1924*Type species*

Tangasaurus mennelli Haughton, 1924: 3.

Tangasaurus Piveteau, 1925: 155.

Tangasaurus menelli Piveteau, 1926: 78.

Tangasaurus minelli Peyer, 1937: 115.

Diagnosis

Neural spines of dorsal vertebrae high and rectangular; height of neural spine of mid-caudal vertebra about 35 per cent greater than length of associated centrum, and about 75 per cent length of associated haemal arch and spine.

Hovasaurus Piveteau, 1926*Type species*

Hovasaurus boulei Piveteau, 1926: 78.

Diagnosis

Skull lacks tabular. 5 cervical, 20 dorsal, 2 sacral and at least 70 caudal vertebrae. Height of neural spines of mid-dorsal vertebrae at least 75 per cent greater than length of associated centrum, whereas height of a mid-caudal neural spine can be more than 125 per cent greater than length of associated centrum; neural spine of mid-caudal vertebra almost 90 per cent length of associated haemal arch and spine. Mammillary processes on neural spines of anterior dorsals. Ribs slightly pachyostotic in mature animals. High number of stones in abdominal cavity suggesting they were used as ballast.

CONCLUSIONS

Tangasaurus mennelli is represented only by three specimens from the Tanga region of Tanzania. Specimens from Madagascar that have been attributed to this species represent a distinct as-yet-unnamed genus that Piveteau (1926) referred to as '*Datheosaurus*' and that is being described by Carroll (1981).

Four genera from Africa and Madagascar are herein assigned to the Tangasauridae. Two subfamilies are recognized on the basis of differences in caudal anatomy. Kenyasaurines were not as highly specialized for an aquatic existence as were the tangasaurines and they were intermediate in morphological specialization between *Youngina* and *Hovasaurus*. Tangasaurids and younginids share a number of derived characters and, therefore, have been united into a single superfamily, the Younginoidea.

Acerosodontosaurus (Currie 1980), *Galesphyrus* (Carroll 1976a), and *Heleosaurus* (Carroll 1976a) have recently been referred to the Younginidae, but they do not possess the derived characters shared by *Youngina* and the tangasaurids. Therefore, they should not be considered as younginoids. Their systematic position will be considered in a separate paper.

The shared derived characters of the Younginoidea are not found as a suite in other eosuchians, which strongly suggests that *Youngina* is not the ancestral morphotype for any eosuchians other than the Tangasauridae.

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Leda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

- (a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
- (b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- (c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

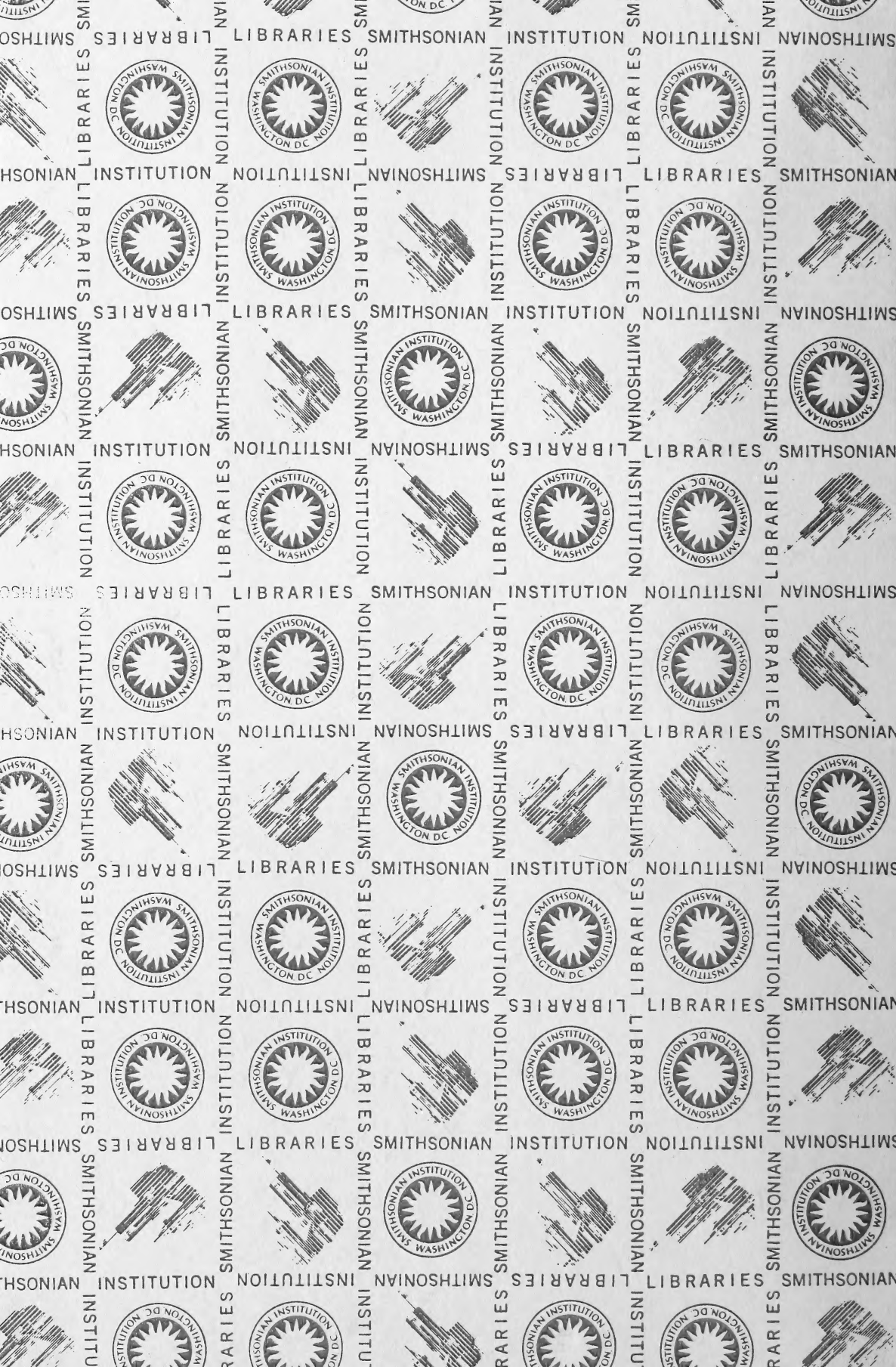
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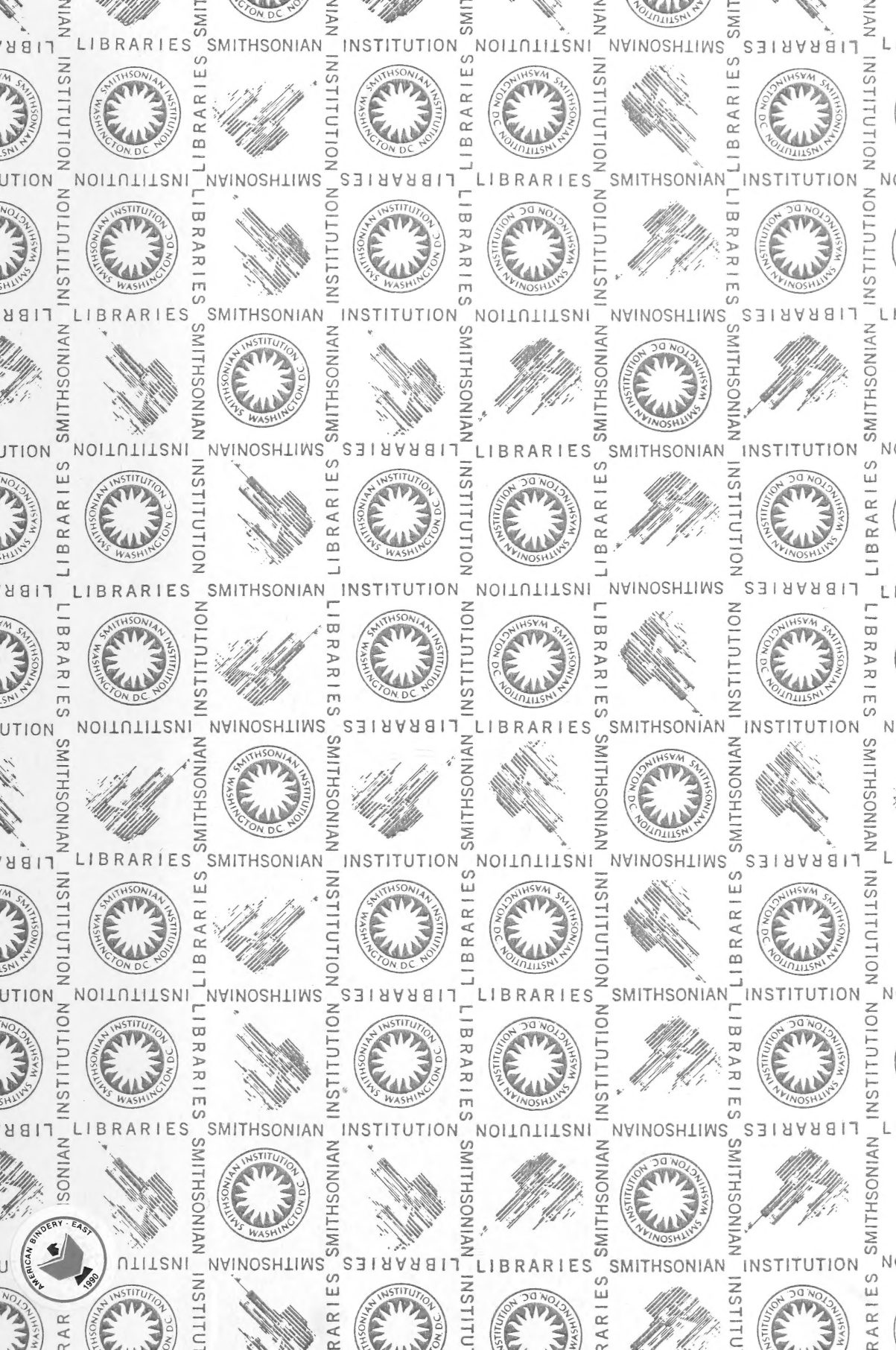
Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

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